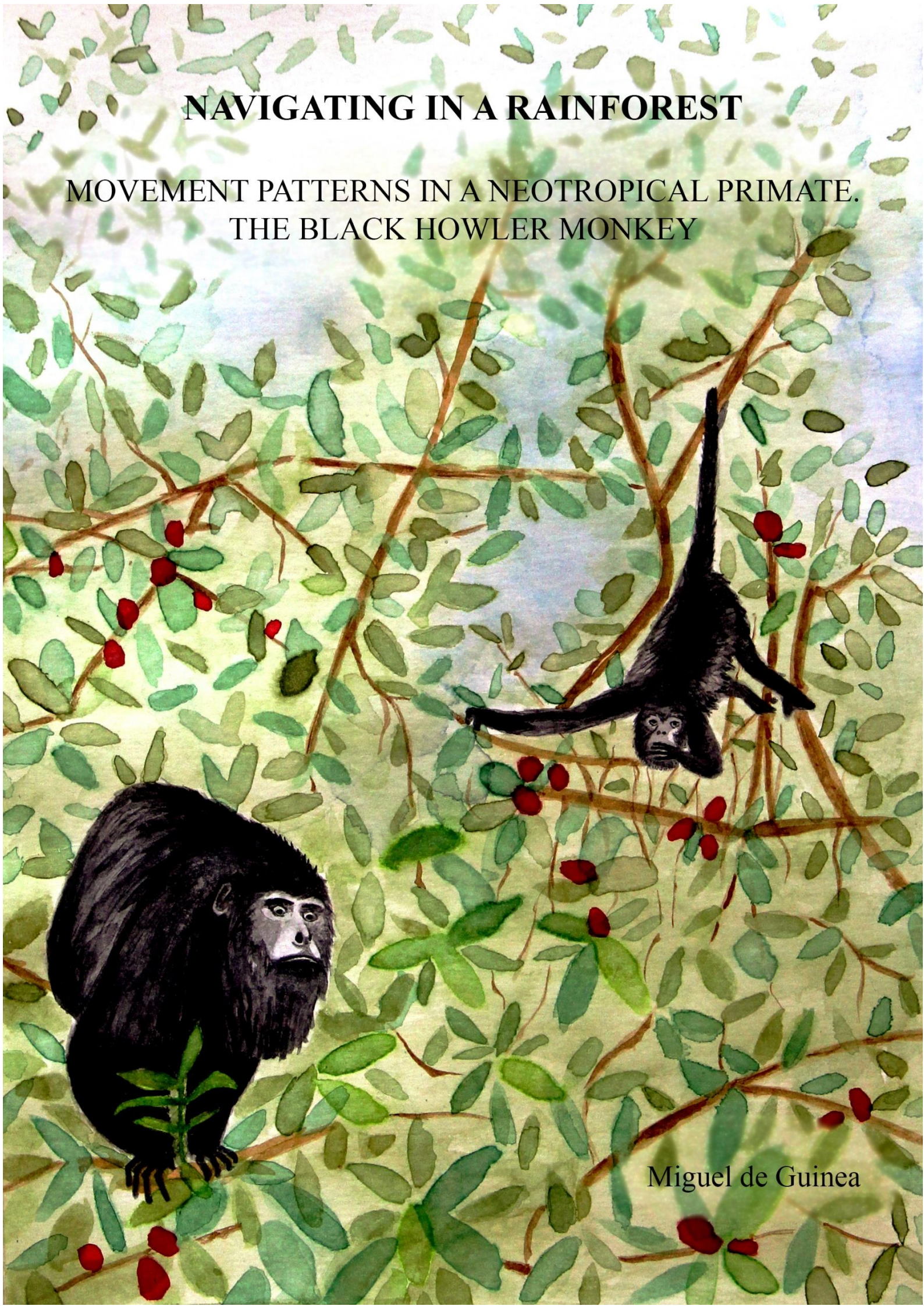
NAVIGATING IN A RAINFOREST

MOVEMENT PATTERNS IN A NEOTROPICAL PRIMATE. THE BLACK HOWLER MONKEY



Miguel de Guinea

Faculty of Humanities and Social Sciences

Oxford Brookes University

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Director of Study: Prof. Dr K.A.I. Nekaris

Second supervisor: Prof. Dr V. Nijman

External advisor: Prof. Dr A.J. Estrada

Caminante, son tus huellas
el camino y nada más;
Caminante, no hay camino,
se hace camino al andar.
Al andar se hace el camino,
y al volver la vista atrás
se ve la senda que nunca
se ha de volver a pisar.
Caminante no hay camino
sino estelas en la mar.

Antonio Machado, 1973

Proverbios y cantares (XXIX)

Wayfarer, the only way

Is your footprints and no other.

Wayfarer, there is no way.

Make your way by going farther.

By going farther, make your way

Till looking back at where you've wandered,

You look back on that path you may

Not set foot on from now onward.

Wayfarer, there is no way;

Only wake-trails on the ocean.

Antonio Machado, 1973

Proverbios y cantares (XXIX)

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Abstract

Navigating rainforests requires a continuous integration and processing of socio-ecological information. To incorporate such information into movement decisions, animals have evolved different cognitive mechanisms that enhance their spatial performance and foraging effort across heterogeneous landscapes. While sophisticated spatial skills are agued to underly flexible and efficient movement patterns, low spatial skills are argued to reflect movement patterns highly conservative and constrained. Here, I investigated different aspects of the navigational strategy of an arboreal, group-living and energy-minimizing Neotropical primate, the black howler monkey (*Alouatta pigra*). Specifically, I explored: (1) how black howler monkeys structure the space wherein they live (i.e., cognitive maps); (2) the influence of landscape features in their movement patterns; (3) their ability to navigate flexibly under varying conditions; and, (4) their ability to remember specific biologically meaningful events within their home range and adjust their movement decisions accordingly. From September 2016 through August 2017, I collected ranging and behavioural data from five groups at Palenque National Park, Mexico, where I marked all individual feeding trees ($N = 931$ trees) from the top ten preferred tree species. My findings first showed that black howlers navigated through routes more frequently than simulated random-walker agents. Second, frequently used routes were associated with potential monitoring of feeding trees and avoidance of energetically costly landscape features. Third, I did not find evidence of navigation flexibility under conditions of increased intragroup competition, knowledge or motivation. Instead, evidence of potential planning behaviour was observed in both locations where intergroup encounters had taken place and in fruit trees with increased phenological synchronicity. Ultimately, this data on the spatial strategies of black howler monkeys are set within the movement ecology framework, highlighting the

importance of route network optimisation and the relationship between cognitive flexibility and memory.

Chapter 1: General Introduction

1.1 Organisation of the Thesis

The structure of this research is centred on the movement patterns of black howler monkeys (hereafter black howlers) in general, and their navigation skills in particular. I start reviewing the bulk of literature on animal movement, which is narrowed down from the combination of factors that influence the motion capacity of animals to the neurophysiological basis of spatial cognition. I emphasise the importance of studying foraging cognition in wild primate populations to answer evolutionary and cognitive questions. Subsequently, I describe the data collection protocol followed during the study period to gather information on black howlers' travelling and feeding behaviour, landscape structure and trees' phenological patterns.

The body of the thesis is composed of four consecutive research chapters. First, I examine the paradigm of cognitive maps in black howlers using network analyses and random movement simulations as novel contributions to the field. Subsequently, I describe the energetic and cognitive advantages of navigating through habitual routes in rainforests and its potential consequences limiting the spatial flexibility during navigation. For this, I apply high-resolution, small-scale landscape analyses controlling for spatial autocorrelation. Finally, I examine the role of past socioecological events on shaping the travelling trajectories of black howlers as a proxy for planning skills.

To conclude, I discuss the implications of this research in the context of an evolutionary trade-off between spatial flexibility and memory mediated by habitat predictability. I summarize potential applications of methods developed and validated here in conservation and trace future lines of research based on newly available technology.

1.2 Animal movement

Ecosystem functioning and species survival are inevitably linked to animal movements and *vice versa* (Lundberg & Moberg, 2003; Tucker et al., 2018). Animals take part as a mobile link in ecological processes such as the ecosystems' chemical cycles (i.e. carbon, nitrogen, sulphur) and trophic chains by determining, with their presence in time and space, the occurrence and distribution of these processes (Rubenstein & Hobson, 2004; Fortin et al., 2005). Moving animals disperse pollen, which allows the germination of multiple angiosperm species (insects, Wiebes, 1979; birds, Johnson & Nicolson, 2008; bats, Fleming & Murray, 2009; primates, Sussman, 1991) and disperse seeds throughout hundreds of kilometres promoting the spatial distribution of fruit trees (Estrada & Coates-Estrada, 1984; Côrtes & Uriarte, 2013). In addition, species richness and biodiversity at a given point at time and space is determined by their own movement creating fluxes of biomass that shape our world at local, regional and global scales (Morales et al., 2010; Jeltsch et al., 2013).

Ecosystems themselves influence animal movements as well, which may either constrain (e.g. mountain ridges, lakes) or promote (e.g. low availability of feeding resources) their ranging patterns (Fagan et al., 2013). Animal species have been evolving a series of strategies to move within and between ecosystems and adapt to the ecological pressures and the physical barriers imposed by the continuously changing landscapes (Milton, 1981; Fahrig, 2007). The evolution of such movement strategies has been hypothesised to optimise the individual's global energetic balance between the benefits of energy acquisition and the metabolic costs of different behaviours (Charnov, 1976). By minimizing the time and energy spent on travelling and maximising the final reward of the travel (e.g. the energetic value of the feeding source), animal species would enhance their fitness against their competitors (Altmann, 1974; Charnov, 1976).

This outcome can be achieved through anatomical, physiological or behavioural adaptations that decrease the time needed for travelling or foraging and, consequently, increase their investment on other activities such as mating, breeding, territorial defence, engaging in social activities or resting (Schoener, 1971; Lehmann et al., 2007; Korstjens et al., 2010).

According to Nathan et al., (2008) animal movement results from a complex set of interactions between the motion capacity and the navigation skills of the individual. Such interactions will be dependent on the particular internal status at a given moment in time (e.g., hunger of the individual) and the influence of external factors (e.g., existence of a physical barrier in the landscape), which will determine the movement decisions of animals (Fig. 1.1). The most basic feature determining an individual's movement capacity is its motility: the structural and functional traits evolved to enhance the spatial movement performance across different media where animals live in (such as air, water or terrestrial habitats; Schaeffer & Lindstedt, 2013).

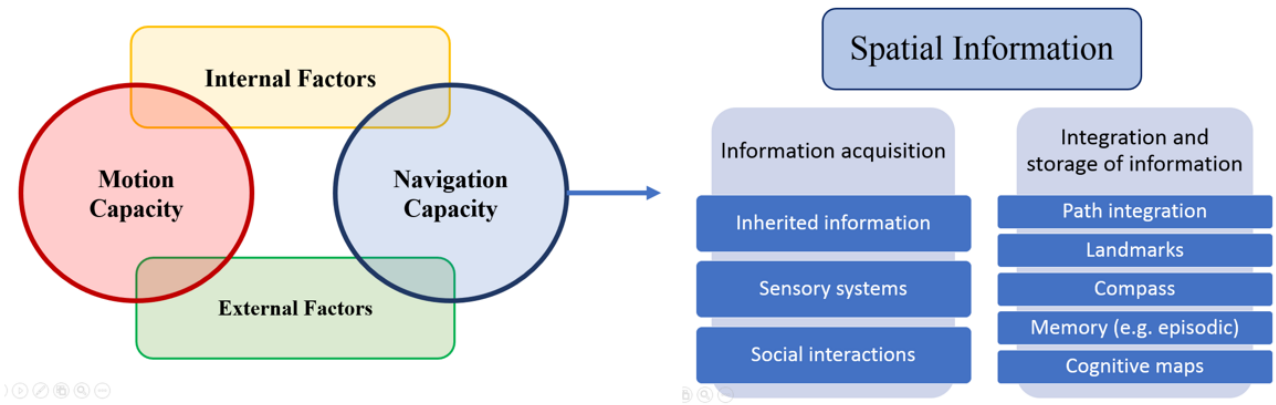


Fig. 1. 1 Schematic representation of the components of the movement ecology framework pointing at the mechanisms to acquire, integrate and store spatial information to navigate

Aquatic environments, which are characterized by high density and viscosity, likely led fishes and cetaceans to evolve caudal spins and tail flukes respectively as hydrodynamic structures to favour their movement (Webb, 1984; Reidenberg, 2007; Fig. 1.1). Although gravity is not the main driver of animal locomotion in water, the main problem for terrestrial animals relies on overcoming gravitational forces as they move, turning body size into a natural constraint for locomotion (Biewener, 1990; Biewener & Patek, 2018). This is why savannah predators (cheetahs, *Acynonyx jubatus*, and lions, *Panthera leo*) are able to increase their ratios of acceleration (37%) and deceleration (72%) more than their respective prey (impalas, *Aepyceros melampus*, and zebras, *Equus quagga burchellii*, respectively) by presenting lower body size and increasing muscular fibres (Wilson et al., 2018).

Since the motor that powers animal movement is the skeletal muscle, small changes on its few muscle components have triggered a diverse range of functional outputs (Schaeffer, 2013). For instance, elevated levels of myoglobin in skeletal muscles increase oxygen retention, which enables longer dive times between breaths in aquatic mammals (Noren et al., 2001). Similarly, aerial animals have double-packed mitochondria within the muscular fibres to increase the production of anaerobic energy and cover the increased energetic demands during flight (Rome & Lindstedt, 1998).

Since locomotion is strictly dictated by the energetic balance of the individual, increasing energetic expenditures on motility will potentially drive a decreased investment on other physiological or behavioural traits (Nathan et al., 2008). In the case of long distance migratory birds, enlarged pectoral muscles allow them to intensify their flying performance (Butler, 2016). All year resident birds present smaller pectoral muscles but a significantly larger brain size than migratory birds (Sayol et al., 2016). Sayol et al., (2016) explained that while resident birds in temperate regions are subject

to high environmental variation in terms of food availability, migratory birds avoid such circumstances. Thus, enlarged brains would allow resident birds to facilitate behavioural adjustments to enhance survival under changing conditions (Sol, 2009). They compensate the substantial energetic and developmental costs of producing and maintaining enlarged brains by not investing energy on prolonged migratory processes (Isler & van Schaik, 2006; Sol, 2009).

The role of the internal status (i.e., age, breeding status, hunger level, personality) of an individual has also been shown to be determinant in the movement patterns of animals (Nathan et al., 2008). Spiegel et al., (2013) showed that free ranging griffon vultures (*Gyps fulvus*) increased their daily flight distances, maximum displacement and flight elevation during the first five days of starvation and decreased the following five days. Thus, vultures performed a flexible response to increasing hunger levels reflecting a trade-off between increasing motivation to find food and the risk of starvation (Spiegel et al., 2013). Similarly, more aggressive blue-tongued skink (*Tiliqua rugosa*) used their core home ranges less frequently than less aggressive individuals probably because of their increased tendency to invest more time on patrolling their home ranges boundaries (Spiegel et al., 2015; Sih et al., 2018; Fig.1.1). In addition, the relevance of external factors such as resource availability, competition or predation risk has also been highlighted within the framework of animal movement ecology (Nathan et al., 2008; Fagan et al., 2013). In the case of lions inhabiting western Serengeti, space use was consistently associated with areas of high prey biomass and vulnerability: lions tended to spend more time in a corridor which had to be taken by their prey in order reach water sources during dry season (Kittle et al., 2015). In fact, their ranging patterns happened to overlap the ones of their main inter-specific competitors, the spotted hyena (*Crocuta crocuta*), which was potentially tracking the movements of lions across their

home range (Kittle et al., 2015). Similarly, Carnaby's cockatoos (*Calyptorhynchus latirostris*) nesting in fragmented areas travelled further from their nests when foraging than cockatoos in continuous vegetation travelled (Saunders, 1980; Fig. 1.1). As a potential consequence, females showed less attentive brooding behaviour and breeding success, which highlights that fragmented landscapes can decrease animal's fitness by changing their movement patterns (Doherty & Driscoll, 2018).

Even with complete information about an individual's internal state and its external environment, we cannot evaluate the efficiency of its movement strategies without taking into account its navigational capacity (Nathan et al., 2008; Spiegel & Crofoot, 2016). Animals' navigational capacity is determined primarily by their ability to obtain information from multiple sources and secondarily by the integration and storage of such information (Fagan et al., 2013; 2017). Information acquisition related with movement decisions in animals can be genetically inherited but also self-acquired via sensory cues or transmitted by conspecifics (Spiegel & Crofoot, 2016). For instance, different migratory species were shown to rely on genetically inherited information, which determined the timing and direction of migratory events (Liedvogel et al., 2011). The case of the eastern North American monarch butterfly (*Danaus plexxipus*) is specially outstanding since three successive generations are involved throughout each migratory event between southern Mexico and Canada (Brower, 1996; Fig. 1.1). Prior migration, environmental changes (i.e., temperature, daylight period) activate specific gene sequences that triggers the beginning of the migratory event but also the heading direction (Guerra & Reppert, 2013). Seemingly, such epigenetic control is maintained during the course of the migratory event over generations and reversed upon arrival (Reppert & de Roode, 2018). Similarly remarkable is the case of the juvenile bristle-thighed curlews (*Numenius tahitiensi*), which are able to migrate 4,000 kilometres for

the first time without any guidance from experienced individuals (Marks & Redmond, 1994).

Likely, most of the information implied on movement-decision making is acquired within an individual's perceptual range. This means that by following gradients (e.g., chemical tapestries, magnetic fields) or cues (e.g., olfactory, visual) an animal can orientate its relative position in space and/or make heuristic decisions about where to go next (Wiener et al., 2011). For instance, measuring changes in the environment of certain chemicals and moving according to these gradients, as *Escherinchia coli* does, is one of the most basic yet still efficient movements described (Berg, 2000). Similarly, green sea turtles (*Chelonia midas*, Lohmann et al., 2004), big brown bats (*Eptesicus fuscus*, Holland et al., 2006) and homing pigeons (*Columbia liva*, Wiltschko & Wiltschko, 2013), among others, base their movement patterns in divergences on the magnetic field of the Earth. Thus, the magnetic field of the Earth acts as a gradient, which animals can use as a compass to orientate their position in space. Similarly, many species rely on visual cues as a compass to orientate their movements (Wiener, 2011). For instance, African ball-rolling dung beetles (*Scaraebus satyrus*) rely on the positions of the celestial visual cues from the Milky way to orientate their movements along straight paths even during clear moonless nights (Dacke et al., 2013; Fig. 1.1). Nocturnal bird migrants such as blackpoll warblers (*Setophaga striata*) also navigate using the stars as a compass (see also harbour seals, *Phoca vitulina*, Mauck et al., 2008), which allows warblers to decrease the probability of finding predators on their way (Emlen, 1975). Other migrant birds were described to navigate during the day guided by the sun instead (Guilford & Taylor, 2014). Importantly, by combining cues from multiple sensory modalities, animals may increase the range and quality of the spatial information they can obtain (Fagan et al., 2017). For instance, bats (Pterodpodidae) can

use multiple sensory cues (visual, olfactory and echolocation) to succeed in their foraging effort (Korine & Kalko, 2005), but also select those signals that represent relevant information and isolate them from the other ones or "noise" (Gomes et al., 2016).

Finally, information acquisition can be transferred from conspecifics or heterospecifics. Group living animals may not only enhance the visual detection range beyond their own physiological limitations but also improve the quality of information by integrating multiple individual's experiences (Ward & Webster, 2016). For instance, honey bees' (*Apis mellifera*) have been suggested to communicate the location (angle and distance) and profitability of recently found feeding sources through a series of rhythmic moves performed in front of conspecifics – the so called "waggle dance" (von Frisch, 1967; Riley et al., 2005; Fig. 1.1). Similarly, African elephants (*Loxodonta africana*) acquired techniques for exploiting specific resource sites by observing conspecifics during extended periods of time (Fishlock et al., 2016). However, this resulted on a high fidelity towards certain sites over generations, even though the quality or accessibility of these sources may decrease over time (Fishlock, 2016).

While information perception is fundamental to navigate, the evolution of neurobiological systems allowed animals to store, integrate and recall spatial information to process more complex spatial decisions based on previous experiences (Milton, 1981; Gallistel, 1990). Even though the role of perceptual cues has been extensively studied (see Mueller et al., 2011 for a review), the mechanisms by which cognitive capacity determines animal navigation patterns and movement decision is still widely unexplored and remains a major challenge within the movement ecology framework (Nathan et al., 2008; Holyoak et al., 2008).

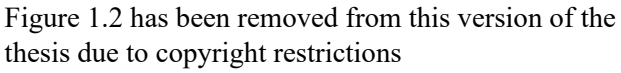


Figure 1. 2 From top to bottom and left to right: blue whale's (*Balaenoptera musculus*) tail fluke; sleepy lizard (Spiegel et al., 2015); Carnaby's cockatoos travelled further in more fragmented forests (right) than in continuous forests (left; Doherty & Driscoll, 2018); Monarch butterfly migration (Liedvogel et al., 2011); dung beetle's navigation in the presence (A) and absence (B) of celestial cues (Dacke et al., 2013); and, honey bees' waggle dance (Riley et al., 2005).

1.3 Navigation

Once spatial information is perceived either via self-acquisition or through social interactions, it is encoded and stored in the neural system where synapsis among specialised cells are created both within the hippocampus and between its closest regions (i.e., the entorhinal region; Moser et al., 2008). These cells, called "place cells" and "grid cells" among others, form the basis for quantitative spatiotemporal representation of places, routes, and associated experiences during behaviour and in memory (Moser, 2008; Moser et al., 2015). Place cells, which are located in the hippocampus, activate in correspondence of a specific region of one's physical environment (O'Keefe & Nadel, 1978). Upstream the hippocampus, in the entorhinal cortex, grid cells activate when the animal is in any of the multiple locations that form a triangular grid (Moser et al., 2015; Fig. 1.2). Thus, grid cells have different period spacings, and they act collectively to form a universal, flexible code for mapping both familiar, but also unfamiliar, space (Sanders et al., 2015). In pragmatic terms, grid cells map out space according to its sensed structure while place cells layer on top of them to add meaningful locations such as foraging sites (McNaughton et al., 2006; Moser et al., 2008). Thus, in combination with other hippocampal cells (e.g., head cells, border cells; Moser et al., 2008; Moser et al., 2015), an animals' brain process algorithms to link places in metric terms supporting the process of movement decision-making (Moser et al., 2008). The cognitive effort employed to encode spatial information will be analogous to the internal representation that animals are able to generate, and it will determine the spatial strategy that will be used to navigate (Garber, 2000).

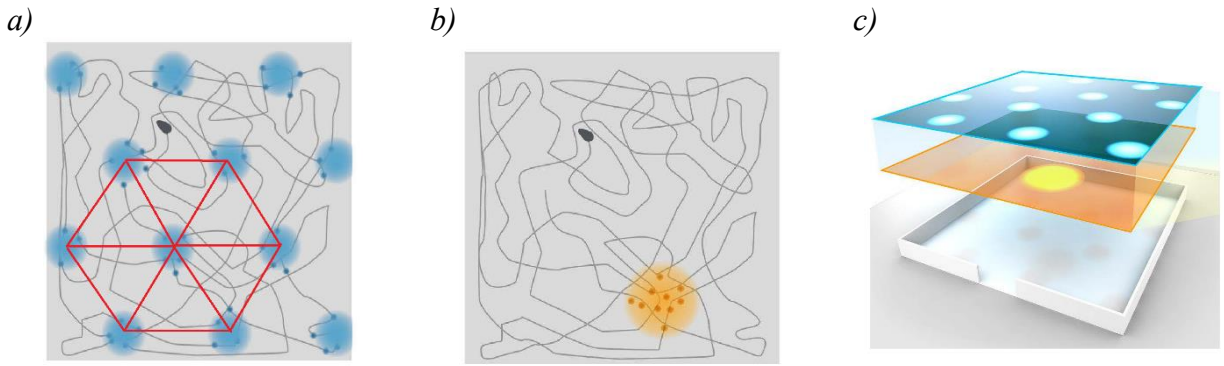


Figure 1. 3 Illustration of the combined mechanism of grid cells and place cells in the entorhinal cortex and hippocampus to represent the space: a) each grid cell fired multiple times when the rat (dark grey) moved through the same location within the cage, creating an hexagonal grid constructed to navigate; b) place cells only fired when a certain location in space is recognized by the rat; c) each cell type acts as a layer of information to determine different locations in the space and allow the rat to make movement decisions (Moser et al., 2015).

Some animals move from one place to other by keeping track of their changing position in space in relation to a selected site while integrating linear and angular self-motion (Tolman, 1948; McNaughton et al., 2006). Thus, animals are able to return to their reference site in a highly efficient manner without making use of familiar position cues (Wehner & Menzel, 1990; Collett & Collett, 2000). This system, called "path integration" (previously known as "dead-reckoning"; Mittelstaedt & Mittelstaedt, 1982), might rely uniquely on grid cells which provide a substrate to navigate and compute homing behaviour efficiently in the absence of visual or olfactory cues (McNaughton et al., 2006). Indeed, eusocial insects are able to calculate the vector in between their current position and their nest by computing the distance and angle in between their previous location and the nest (Collet & Collet, 2000). This strategy allows ants and honey bees to travel large distances from their nests in comparison to their body size in order to find food sources and return to their nest using shorter and more direct paths (Collett & Graham, 2004). In a classic experiment performed by

Piéron (1904), ants (*Messor barbus sancta*) were displaced to further areas while they were returning to their nest, and they continued performing the same path as if they had not been moved. When their trajectory reached the point in which the animal would have found its nest, it started searching for the nest again (Piéron, 1904, mentioned in Collet & Collet, 2000).

Mammals and birds with a fixed home base rely on path integration to navigate within their home range as well (Etienne & Jeffery, 2004). However, path integration in mammals and birds does not depend only on self-motion cues alone but also on familiar external references, which lead animals to perform more accurate and flexible movements (Cheng & Spetch, 1998). Reliance on external visual cues depends on place cells, which activate when the animal recognizes a certain location in space, providing the basis for associative memory (McNaughton et al., 2006; Killian et al., 2012). As mentioned above, information attached to visual cues can be acquired either genetically (e.g., following the sun as a compass to migrate, Perdeck, 1958) or via self-experience (e.g., associating landmarks within a home range to locate feeding sources, Garber & Brown, 2006). The integration of both mechanisms (path integration and landmarks) in Mongolian gerbils (*Meriones unguiculatus*; Collett et al., 1986) allowed them to successfully follow a trajectory to obtain food rewards in total darkness after having learned the location of a series of beacons. Gerbils were able to associate physical properties of landmarks with different types of rewards after having learnt the distance and directions between such landmarks (Collett et al., 1986). By combining path integration and landmarks accurate navigation can remain in the absence of one or the other (Etienne, 2004). However, the number of landmarks that can be remembered and associated to feeding sites depends on the cognitive power of the animal. Consequently, some species have developed strategies to minimize the cognitive effort required to

memorize multiple locations while still locating feeding sources within their habitat (Wiener, 2011). For instance, scatter hoarders face the problem of creating a diverse and ephemeral distribution of caches whose location has to be remember accurately enough to retrieve later (Delgado & Jacobs, 2017). By placing seeds from the same bearing tree together, they reduce the load of information (i.e., locations) to remember while the accuracy of retrieval would increase (strategy called "spatial-chunking"). Wild fox squirrels (*Sciurus niger*) were described to engage in such chunking strategy when there was a central food source that acted as a cognitive anchor but on its absence they followed simple heuristic rules (Delgado & Jacobs, 2017).

The same neural mechanism that is used to associate landmarks to feeding sites also serves to link and recall self-experienced events in the context of both space and time to certain locations (Buzsáki & Moser, 2013). This process is called "episodic memory" and stores information regarding social events, fruit productivity and/or predatory presence (Clayton & Dickinson, 1998; Janson, 2016). Notably, the mechanism used for coding a path across an environment is similar to the mechanism used to represent sequences of events in episodic memory: neurons fire sequentially along a linear path in the same way that the elements that build up episodic memory are dominantly linked unidirectionally (Buzsáki & Moser, 2013). Indeed, brain imaging revealed that the neural systems involved in navigation overlap with the systems involved in episodic memory, route planning and imagination (O'Keefe & Nadel, 1978; Burgess et al., 2002). By associating episodic memory with navigation, animals might be able to plan their future ranging patterns according to previously lived experiences (Schacter & Addis, 2007). Thus, the more complex, flexible, and temporally extensive episodic memory is, the more advantageously animals will plan their movements and enhance their navigation (Klein et al., 2010; Buzsáki & Moser, 2013). For instance, scrub jays

(*Aphelocoma coerulescens*) showed the remarkable ability of not only identifying which cache was hidden where, but also to predict when they should return to pick it up (Clayton & Dickinson, 1998; Raby et al., 2007). Similarly, chimpanzees (*Pan troglodytes*) were able to remember the location of more productive fruit trees and trees that produced fruits that contained high amounts of sugar over years, but also social events that took place at these feeding locations and shape their ranging patterns according to these memories (Janmaat et al., 2013; Ban et al., 2016; Janmaat et al., in prep.). Chimpanzees and scrub Jays use this information to plan their ranging patterns and anticipate not only *what* they will feed *where*, and *when* they should visit it, but also for *how long* it will be available (Raby, 2007; Janmaat et al., 2014).

Emery & Clayton (2004) highlighted that even though primates are often the focus of cognitive studies due to their close evolutionary relationship with humans, other relatively large brained animals such as corvids also have complex cognitive skills (e.g., tool manufacture, mental time travel). Parrots (Psittaciformes) together with corvids represent the avian lineages with larger brain sizes, which also allow them to engage in more complex social relationships and imitate the human speech (Emery & Clayton, 2004). Among mammals with increased brain size, dolphins (Odontocete) can flexibly access memories of past events and construct sophisticated representations of the world and themselves (Marino et al., 2002; Mercado III & DeLong, 2010). Dolphins' decisions are guided by the perceived impact of their actions based on what they remember, demonstrating not only the use of episodic memory but also their planning skills (Mercado III, 2010). Similarly, elephants (Proboscidea), which possess remarkable large brains in relation to their body size, have an outstanding long-term memory, plus an extensive spatiotemporal and social memory that allow them to navigate efficiently throughout their habitat (Hart et al., 2008; Bates et al., 2008).

Primates' abilities – especially apes – to represent the external world and place a complex set of memories over it to navigate and enhance their foraging effort have been argued to be the basis of modern human intelligence (Milton, 1981; Dolins & Mitchell, 2010; de Waal & Ferrari, 2010). However, it is primordial to keep in mind that not only other taxonomic lineages possess sophisticated spatial skills but also increments in relative brain size depending on their each taxa (Jerison, 1970; Logan et al., 2018).

1.4 Foraging Cognition in Primates

Rainforests harbour the highest diversity and richness in tree species of the world (Reich, 1995). However, the distribution of tree species is not homogenous within rainforests since their location depends on both biotic (e.g., seed disperser population dynamics) and abiotic factors (e.g., weather conditions) that condition their emergence and survival (Janson & Chapman, 1999; Meier et al., 2010). Similarly, trees species' phenological cycles are highly variable: some species only produce fruits during certain months of the year while other tree species have individuals ripening asynchronously throughout the entire annual cycle (Chapman et al., 1999a; Janmaat et al., 2016). In fact, some tree species present supra-annual cycles of fruit production, which can difficult the predictability of fruit appearance of these tree species (Chapman et al., 1999b; Janmaat et al., 2016). Thus, in tropical forest fruits are available during very specific time intervals, and when they are, many animals compete over this high energetic, sugary food (Houle et al., 2007). Despite this, most primates strongly rely on fruits as their main feeding source that supports their energetic needs and balances their nutritional requirements (Lambert, 1998), primates are successful vertebrate in most undisturbed rainforests (Chapman et al., 1999a).

The evolution of a trichromatic colour vision among the African monkeys and great apes may have helped them to find more easily young leaves and ripe fruits by discerning red-green colours against the foliage (Dominy & Lucas, 2001; Carvalho et al., 2017). Similarly, olfactory cues are typically used by primates to detect fruits within a tree and to assess the quality of the feeding item (Nevo & Heymann, 2015). However, most of the Neotropical and strepsirrhine species do not possess trichromatic colour vision (Osorio et al., 2004; Carvalho et al., 2017). In addition, Schmidt et al., (2010) argued that visual and olfactory stimuli can be unreliable cues over long distances in heterogeneous habitats such rainforests. The longer the distance travelled by a signal in a heterogeneous landscape, the more "noise" will intercept along the way potentially modifying the original signal and distorting the information received by the animal (Schmidt et al., 2010). Therefore, primates were argued to rely on enhanced cognitive skills to locate, update and recall feeding sources, likely provided by an unique trait that characterizes the Order Primates: their enlarged brain size in relation to their body size (Clutton-Brock & Harvey, 1980; Milton, 1981; DeCasien et al., 2017). Brain tissue is metabolically expensive not only to be generated but also to be maintained, and it requires a continuous and reliable flow of nutrients to function adequately (Martin, 1981; Isler & van Schaik, 2006). Hence, any increase in relative brain size may only be possible in populations that have managed to either improve their access to nutrient or decrease other existing energetic demands (Isler & van Schaik, 2006; DeCasien & Higham, 2019). By feeding on high quality, easily digested food sources such as fruits, primates may have increased their net energetic gains while decreased the metabolic costs of digestion (Clutton-Brock & Harvey, 1980). Thus, as Milton (1981) first exposed in her "Ecological brain theory", fruit consumption allows the construction and

maintenance of enlarged brains, which might provide cognitive advantages to better locate feeding sources against its competitors.

Even though relative brain size has been widely used a proxy for cognitive skills, its adequacy has been debated during the last decades (Byrne, 1996; Herculano-Houzel, 2011; Navarrete et al., 2011; Logan, 2018). Azevedo et al., (2009) proved that larger primate brains contained higher neuronal numbers than smaller primate brains. In fact, the number of neurons present across primate species increases by a power function of 1.1 million neurons for each brain's gram (Gabi et al., 2010). Such scaling rule is different for each animal lineage, so that species with similar brain size but coming from different evolutionary lineages will differ in the number of neurons present within their brains (e.g., the brain size of the agouti, *Dasyprocta sp.*, and the owl monkey, *Aoutus sp.*, are18 grams and 16 grams, but their neural numbers are 857 million and 1.468 million respectively, Herculano-Houzel, 2009). Since Moser et al., (2008) showed that specialised neurons present in the hippocampus are in charge of encoding spatial information, presumably species with more neurons will increase the number of synaptic connections leading to a more accurate and precise use of spatial information. In addition, experimental and empirical evidence has frequently shown that great apes outperform their relatives in cognitive tasks (Boesch & Boesch, 1984; Tomasello & Call, 1997; Deaner et al., 2007; Normand & Boesch, 2009; Amici et al., 2012; Janmaat et al., 2014; Rosati, 2017), suggesting that relative brain size may still be used as a reliable indicator of cognitive power within primate taxa.

Based on this assumption, DeCasien et al., (2017) performed the largest analysis to date testing the effect of different potential ecological and social pressures on primates' brain size across more than 140 species. The only factor that predicted relative brain size in the model was diet, suggesting that level of frugivory is indeed a major driver on

brain cognitive evolution and human intelligence (DeCasien et al., 2017; see also Powell et al., 2017). Further, fruit consumption is linked to brain size and cognitive performance across different primate lineages (Rosati, 2017; Tujague & Janson, 2018). Malagasy lemurs and African lorises increased brain size with seasonality suggesting that larger brains allow strepsirrhines to perform more flexible behaviours to find preferred feeding sources under disadvantageous conditions (van Woerden et al., 2010). Similarly, frugivorous lemur species, which were shown to have larger brains (e.g., ruffed lemur, *Varecia variegata*; MacLean et al., 2009) than their folivores counterparts (e.g., Coquerel's sifakas, *Propithecus coquereli*), outperformed the latter across three tasks targeting different aspects of spatial memory (Rosati, 2017). In Neotropical primates, brain shape diversification was suggested to be the result of an early differentiation due to ecological factors such as diet, followed by several shifts determined by group size, which led to a convergence in brain shape across Platyrrhini (Aristide et al., 2016). For instance, capuchin monkeys, whose relative brain size is among the largest of the Neotropical primates, show a remarkable tool use ability akin to chimpanzees' and show impressive spatial memory skills (Visalberghi et al., 2015; Tujague & Janson 2018).

The relationship between degree of frugivory and relative brain size is also found in great apes. Western lowland gorillas (*Gorilla gorilla gorilla*) are highly frugivores while mountain gorillas (*G. beringei beringei*) relies on a folivorous diet probably because of the lack of fruit availability within their elevated habitat (Robbins & McNeilage, 2003; Ganas & Robbins, 2004). As a consequence of the divergence in the distribution and abundance of both fruit and herbaceous feeding sources between both species' habitats (Robbins & McNeilage, 2003), mountain gorilla's home range is smaller than lowland gorilla's home range (Caillaud et al., 2014). The increased

frugivory and home range size in lowland gorillas has been argued to be the driver of their enlarged hippocampus and cerebellum size (Barks et al., 2015) since both factors increase the demand on spatial memory (Eichenbaum et al., 1999). A similar pattern is found between bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*), which share similar social structures and ecological niches (Hohmann et al., 2006). However, chimpanzees rely on more patchily and scarce feeding sources such as fruits while bonobos base their diets on more homogeneously distributed feeding sources (Hohmann et al., 2006; Janmaat et al., 2016). As among gorilla species, the hippocampus of chimpanzee is larger and more symmetrical than bonobo's hippocampus, which is also better connected with other regions of the brain in the former species (Hopkins et al., 2009). This is reflected in the enhanced performance of chimpanzees against bonobos at tracking the distribution of rewards in space and understanding physical causality (Herrmann et al., 2010).

With these characteristics in mind, how do large brains improve primate navigation? According to the ecological brain hypothesis, large brains might allow primates to create sophisticated mental representations of the space over which self-experienced memories and other sources of information are projected to improve movement decisions (Tolman, 1948; Milton, 1981; Garber, 2000). Such representations, called "cognitive maps", are structured in the hippocampus and the entorhinal cortex and allow primates to locate their position in space, predict certain events and plan their travelling behaviour (O'Keefe & Nadel, 1978; Poucet, 1993; Bennett, 1996). Thus, the more complex the neural system is (i.e., number of layers, neuronal connections, brain architecture), the more sophisticated primates' cognitive maps are expected to be (Poucet, 1993). While some primates would tend to follow a set of established routes and based their movement decisions on perceived landmarks, primates with larger

brains might accurately compute distances and directions to their goal from any starting point in space (Garber, 2000; Garber & Dolins, 2014). Hence, multiple species of monkeys and strepsirrhines have been proposed to use the so-called "route based map" (Milton, 1981; Di Fiore & Suarez, 2007; Hopkins, 2011; Lührs et al., 2009), while apes might be using a "coordinate based map" (Asensio et al., 2011; Normand & Boesch 2009; Salmi et al., 2020).

Surprisingly, the increasing growth in the literature on animal cognitive maps has highlighted that various primates species combine both cognitive maps (Trapanese et al., 2019). For instance, the same species was shown to navigate using a route based map and a coordinate based map in different field sites (e.g., chimpanzees in Tai Forest and Kibale National Park; Normand & Boesch, 2009; Bertolani, 2013), different ecological situations (e.g. black capuchin monkeys, *Sapajus nigritus*; Presotto & Izar, 2010) and even under different visibility conditions (Weddell's saddleback tamarins, *Saguinus fuscicollis wedelli*; Porter & Garber, 2013). Some primate species seem to rely on routes more often under periods of food scarcity and low visibility in order to ensure their foraging success, but still perform more flexible ranging pattern under less constrained ecological conditions (e.g., white-faced capuchin monkeys, *Cebus capucinus*, Urbani, 2009; black capuchin monkeys, Presotto & Izar, 2010). Hence, instead of considering a dichotomy in the use of cognitive maps, an increase on brain size could be driving a gradient of flexible ranging patterns across the primate taxa (Warren, 2019). While small-brained primates will be highly constrained to use a fixed set of routes, large-brained primates will have the possibility of performing novel short-cuts but still use routes to facilitate their travel (e.g., chimpanzees, Bertolani, 2013). In line with this, some studies have shown the importance of measuring other ecological variables that may influence primate ranging pattern and mask their cognitive abilities

(Garber, 2000). For instance, arboreal primates depend strongly on the structure of the rainforest and the characteristics of the canopy to navigate (Hopkins, 2011; McLean et al., 2016). Similarly, the energy required by primates to move across landscapes depends on the influence of human activities and proximity to steep ridges among other factors (Gregory et al. 2014; Howard et al., 2018). Taking these factors into account would provide a clearer picture to understand the cognitive evolution across primate species.

Interestingly, human's ability to navigate is also described as a combination of strategies that incorporate landmarks, routes, detours and other orientation mechanisms (Foo et al., 2005; Burgess, 2006; Krasnow et al., 2011; Buzsáki & Moser, 2013). For instance, Australian aboriginal people accurately determined the direction for places that could be over 300 km (Dasen, 1984) but North Americans were not able to correctly point at objects placed in the same room after being blindfolded and disoriented (Wang & Spelke, 2000). Indeed, western humans inhabiting urban settlements have been described to strongly rely on landmarks when travelling (Byrne, 1979; Foo et al., 2005), while many hunter-gatherer societies are able to accurately compute directions and distances in novel spaces (Krasnow et al., 2011; Jang et al., 2019b). The relevance of following prey, locating feeding trees and returning to camp together with culturally transmitted information on how to navigate may have preserved the cognitive abilities to accurately move within the forest (Henke, 2007). Burgess et al., (2006) argued that humans in western societies may still be able to use more complex cognitive skills depending on the amount of self-motion, the structure of the environment and their prior experience on such environment. Thus, humans may be combining both mapping systems in parallel and adapting the cognitive effort according to environmental requirement and their life experiences (Jacobs & Schenk, 2003;

Burguess et al., 2006; Krasnow et al., 2011). As other primates, humans might rely on movements that are not cognitively demanding under specific circumstances but may still be able to perform flexible movement patterns when needed.

1.5 The present study: howler monkeys and navigation

The genus *Alouatta* (Atelidae, Lacépède. 1799), known as howler monkeys or howlers, represents the group of Neotropical primates with the largest spatial distribution (from Argentina to Southern Mexico: nearly 6.000 km in straight line, Kowalewski & Raño, 2017). This diurnal group of primates is characterized by their prehensile tails, which are used as supports while eating or resting (Bergeson, 1998), and their enlarged hyoid bone, which allows them to produce impressively loud calls (Schön, 1971). The formation of the Andean Rift 8 million years ago divided the ancestral population of howlers giving rise to two different evolutionary lineages: North American howlers and the Mesoamerican howlers (Ford, 2006). To date, twelve different species of howlers have been described with considerable morphological (e.g., colouration, body size) and behavioural variation among them (Cortés-Ortiz, 2017).

The social unit of howlers varies from bisexual pairs to unimale and multimale groups, and it may depend on group size, habitat quality and population density (Van Belle & Bicca-Marques, 2015). Generally, both males and females disperse from their natal groups after reaching their reproductive status but this pattern may be changing due to habitat fragmentation (Van Belle et al., 2012). Indeed, howlers successfully inhabit a wide variety of habitats in various states of degradation and size (Van Belle & Estrada, 2006; Arroyo-Rodríguez & Dias, 2010; Bridgeman, 2012). This is possible because of their flexible dietary patterns, which led Silver et al. (1998) to describe them as "facultative folivores" (see also Dunn et al., 2010). This means that even though

howlers can increase the proportion of leaves in their diet according to changing conditions in their environment (more than 80% of their diet was composed by fruit during some months; Pavelka & Knopff, 2004), fruit consumption is still their main option (Plante et al., 2014). During periods of increased leaf consumption, howlers need to increase their resting time as an energetic trade off toward favouring the processing of leaf compounds (Rangel-Negrín et al., 2018). Their enlarged digestive systems allow howlers to break down many different food items but their digestion period can increase to 20±3.5 hours (Chivers & Hladik, 1980; Milton, 1984). This long digestion allow howlers to remain in small fragments with low food availability but implies that less time and energy can be allocated towards other activities such as mating, breeding or socializing (Pavelka, 2004). On the other hand, fruit consumption increases the net energy gain and nutrient acquisition in black howlers while reducing the metabolically expensive processing of leaves in the gut (Lambert, 1998). In addition to the importance of fruit in howlers' diets, Behie & Pavelka (2015) explored the impact of fruit on howler's population dynamics and behaviour. It was suggested that after a prolonged period of fruit shortage, howlers were not able to find alternative feeding sources of readily available energy to sustain their survivorship and reproduction (Behie, 2015). Hence, population density could be determined by pronounced periods of fruit shortage throughout the year.

Howlers are the only Neotropical (Parvorder: Catarrhini) primates with predominant colour vision (Jacobs et al., 1996). By encoding at least two of the genes required for trichromacy in the X-chromosome, howlers systemically inherit the capacity of differentiating between green, yellow and red (Jacobs, 1996; Carvalho, 2017). Behavioural observations have suggested the role of olfaction to discriminate conspecifics in proximity (Baltisberger et al., 2003). However, there is no physiological

evidence of howlers' olfactory sensitivity in terms of detection threshold (Hernández Salazar et al., 2015), while their visual range has been estimated in *ca.* 35 m within tropical forests (Milton, 1981). Since howlers' diet is mainly composed by fruits and leaves, their enhanced visual abilities might provide advantages on distinguishing ripe fruits and young leaves against the background foliage, enhancing their foraging success (Osorio & Vorobyev, 1996; Osorio et al., 2004).

While the evolution of sensorial adaptations benefits the acquisition of food resources, howlers have been shown to rely on their cognitive skills during foraging as well. For instance, Hopkins (2016) demonstrated that mantled howlers in Panama incorporated information regarding the spatiotemporal distribution of fruit availability in their movement decisions. Similarly, howlers have been shown to incorporate social (Van Belle & Estrada, 2019), ecological (Plante, 2014) and physical (Ceccarelli et al., 2019) sources of information into their movement decisions highlighting their ability to compute complex cognitive processes to adjust their ranging patterns. Despite of being among the most studied primate taxa in the Neotropics (Tujague & Janson, 2018; Galán-Acedo et al., 2019), research on howlers' spatial cognition has mainly focused to three taxa (*A. palliata, A. caraya and A. guariba clamitans*; Fortes et al., 2015). Since howlers are experiencing a high and unprecedented rate of habitat loss throughout most of their geographic distribution (Estrada et al., 2017; Bicca-Marques et al., 2020), exploring their spatial skills in their natural conditions is not only necessary to elucidate the conditions that gave rise to the evolution of cognition but also urgent (Janmaat, 2019).

In the present study, I conduct a navigation study on five wild groups of black howlers, *Alouatta pigra* (the largest number of study groups in a navigation study on a Neotropical primate to date, Tujague & Janson, 2018). For this, I aim to address

different aspects of their ability to mentally represent the space, the benefits associated with their navigation strategy, their ability to optimize their movements and their capacity to and recall past experiences associated with specific locations.

In the first chapter, I describe the use of cognitive maps in black howlers. I aimed to elucidate black howlers' tendency to navigate using either a route or a coordinate based map by running computational simulations of random movement as control against which to compare the observed movement patterns. Specifically, I calculated for both observed and simulated movement patterns: (1) the total distance overlapped within habitual route segments; (2) the tendency to revisit feeding sites through the same direction (i.e., cluster of approaching and departure directions); and, (3) the existence and connectivity of nodes intersecting habitual routes. I expected that random walkers would not show patterns of inter-path overlap, clustered revisited directions nor nodes usage, while black howlers would show positive results for all these questions.

In the second chapter, I explore the benefits associated with navigating using a route network. I hypothesised that black howlers inhabiting a variant landscape may have optimised the location of routes to enable them to monitor potential feeding sources while minimizing their energy expenditure. For this, all individual trees belonging to howlers' top ten preferred feeding species were marked in each one of the home ranges and landscape analyses using a detailed topographic map were conducted. Subsequently, I examined the spatial association among habitual routes, visibility of potential food resources and landscape features (i.e., slope, elevation, substrate availability).

In the third chapter, I explore the ability of black howlers to engage in flexible movement patterns regardless of navigating through route networks. I expected that under conditions of increased internal motivation (i.e., hunger), intragroup competition or knowledge, black howlers would travel in a straight manner to gain access to food resources. In addition, I assessed the annual variability of food resources in the area using satellite imagery. I expected that under conditions of reduced food availability, black howlers would increase the linearity of their movement patterns towards food resources.

In my last research chapter, I assess the influence of socioecological information on black howlers' planning skills by examining intentional travelling (i.e., goal-directed behaviour) towards specific locations linked to social and ecological contexts. First, I inferred intentionality by detecting significant directional changes along travel trajectories. Second, I determined at these locations: (1) the behaviour of the group; (2) the occurrence of previous social events; and, (3) the ecological properties of the feeding tree (i.e., food preference, level of phenological synchrony). I expected that after having encountered neighbouring groups at specific locations, black howlers would return to these locations in a goal-directed manner to engage in loud calling behaviour. Similarly, I expected black howlers to plan revisits to specific fruit feeding trees according to their level of preference and phenological synchrony.

Chapter 2: General Methods

2.1 Study site

Palenque National Park (hereafter PNP), 17° 27’ 52’’ - 17° 30’ 10’’ N, 92° 01’ 48’’ - 92° 01’ 48’’ E, is one of the three national parks of the state of Chiapas, southern Mexico, which was created in 1981 and covers a total of 1,171 ha (Diaz-Gallegos, 1996; Fig. 2.1). Diaz-Gallegos (1996) described PNP as composed by 769.4 ha (43.4%) of induced pasturelands, 597 ha (33.37%) of evergreen forest and 387.3 ha (21.8%) of secondary forest vegetation. The remaining area is occupied by covered and uncovered ancient Mayan temples (509 AD, Barnhart, 2001). There are approximately 241 tree species and 484 angiosperm species, of which the genera *Psychotria*, *Ficus* and *Piper* account for the higher number of species (Diaz-Gallegos, 1996; Gómez-Dominguez et al., 2015).

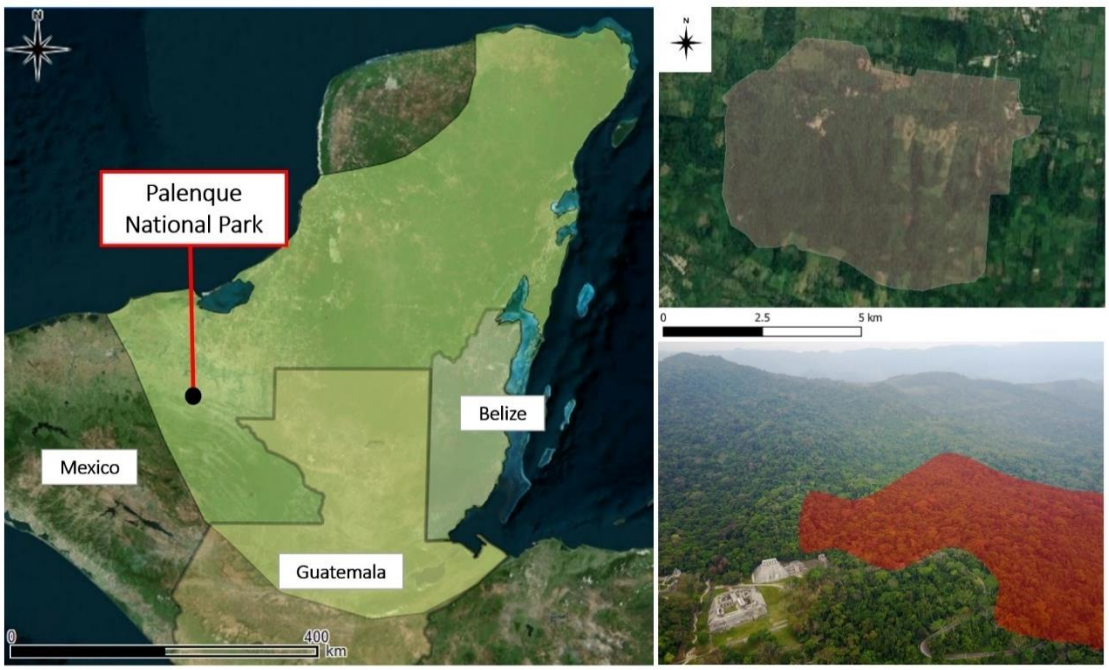


Figure 2. 1 Geographic distribution of *Alouatta pigra* (data from IUCN, 2019; left); satellite view of Palenque National Park (top right) and drone image of the study area within Palenque National Park in April 2017 (covered in red, bottom right).

Palenque has a relatively stable average temperature all year round of approximately 26.4 ± 2°C (T_{max}= 31.7°C; T_{min}= 20.9°C) although there is an annual peak of temperature in between the months of March and May, when average daily temperature increases between 2.0-3.1 °C (CONAGUA, 2019). Rainfall is asymmetrically distributed throughout the year with a rainy season between June and October ($P_{mean\ 1971\text{-}2000}$= 294.7 ± 71.26 mm) and a dry season from November to May ($P_{mean\ 1971\text{-}2000}$= 134.6 ± 56.95 mm; CONAGUA, 2019).

2.2 Study period and observers

From September 2016 to August 2017, two groups of observers followed simultaneously two different groups of black howlers every week, for four days a week. On average, we collected 10 h 21min of observations per study day under different climatic conditions. Since we were collecting data on five different groups of wild black howler, we divided sampling intervals in units of three weeks so that all groups would be sampled once during each sampling unit. Within each sampling unit, the order of the groups was randomly assigned so that we would avoid collecting data in the same group at a fixed temporal interval (Fig. 2.2). Thus, five sampling units, which were constituted by three sampling weeks each, formed a sampling cycle. Throughout the study period we managed to complete four sampling cycles, equalling 45 weeks of observations. All groups of black howlers were habituated to anthropogenic presence. Despite the fact that each observer group was formed by 3–7 international assistants (led by Dr Sarie Van Belle, Elsa Barrios and Miguel de Guinea), none of the study groups showed behavioural modifications as a consequence of increased number of observers.

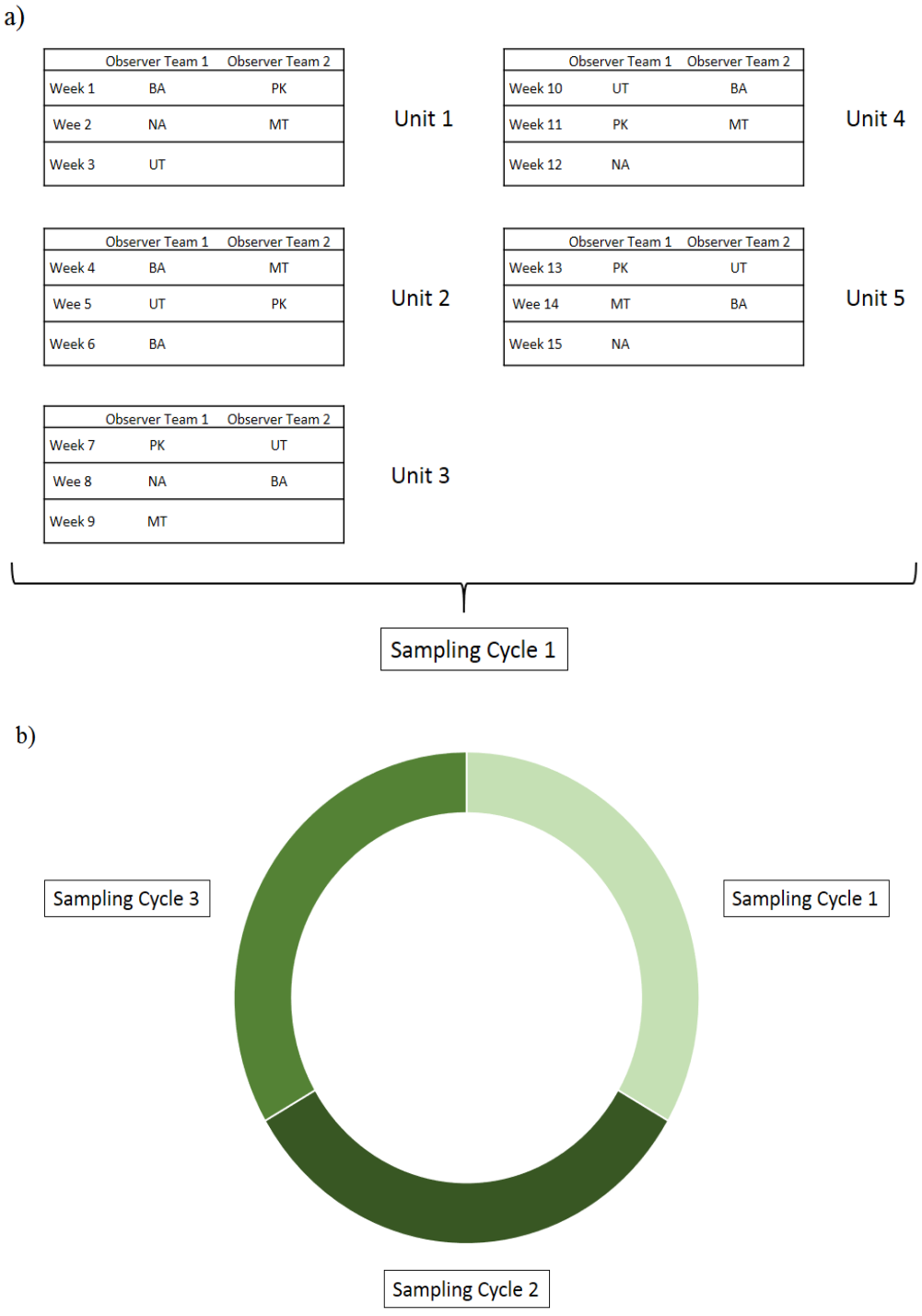


Figure 2. 2 Data collection was performed in two groups of black howlers simultaneously followed by two teams of observers. Once the five different groups of black howlers (i.e., Motiepa: MT; Naha: NA; Pakal: PK; Unites: UT; and, Balam: BA) had been followed a sampling unit was completed and the order in which the groups were sampled in the next sample unit was randomized (a). After repeating the same procedure for five different sample units, we had completed a sampling cycle which encompassed nearly 4 months (15 weeks). Throughout the study period we completed three consecutive sampling cycles (b).

2.3 Study groups

There are approximately 20 groups of wild black howlers around the archaeological site of Palenque, reaching an estimated density of 23 individuals/km^2 (Estrada et al., 2002). From this population of wild black howlers, seven neighbouring groups have been followed up for the last ten years (i.e., Van Belle et al., 2009; Van Belle et al., 2014).

In the present research we selected five groups (i.e., Balam, Motiepa, Pakal, Naha, Unites), which were composed of between 3-12 individuals each, including a central adult male, a central adult female and their offspring (Van Belle et al., 2012; Table 2.1). The composition of some groups changed throughout the study period because of the dispersal of some individuals and the arrival of newborns. One of the study groups, Balam, was not as stable as the other groups and its composition and ranging area changed dramatically in between December 2016 and January 2017. Because of this, data collected on Balam was splitted as "Balam 2016" and "Balam 2017" in the analyses when required (Table 2.1).

Table 2.1 Composition of each studied group between September 2016 and September 2017

	Adult(s)		Sub-adult(s)		Juvenile(s)	Infant(s)
	Male	Female	Male	Female		
Balam16	1	2				1*
Balam17	2	2				
Motiepa	2	2		1	1	2*
Naha	1	2	1		1	3*
Pakal	2	3		1	2	3*
Unites	1	1		1		1

[1]: some of these infants were born during the study period but died after a few months

2.4 Data Collection

2.4.1 Behavioural observations and marked trees

During observation days, we conducted instantaneous scan samples at 15 min intervals from the moment we found our focal group until sunset (*ca*. 5:30 – 17:00 hrs; Altmann & Altmann, 1977). We identified every visible member of the group and recorded all primary behaviours (i.e., resting, feeding, travelling, loud calling) and other behaviours of interest (i.e., grooming, playing, aggressive behaviours, drinking). If an individual changed its behaviour during the minute of the group scan, we selected the behaviour that was predominant during that minute.

In order to obtain detailed information on feeding behaviour, we collected additional group scans for feeding behaviour every 3 min as well (Amato et al., 2013). We started recording feeding scans whenever one or more individuals fed on a plant for a minimum of 5 min accumulated across all feeding individuals in the group (e.g., one individual for 5 min, two individuals each for 3 min, five individuals each for 1 min). If members of the same group started feeding on different plant species, we recorded as many independent food scans as plants the monkeys were feeding on. For each feeding bout, we recorded the item fed on (i.e., mature fruits, young fruits, mature leaves, young, leaves, flowers, petioles, stems), the tree species, and at 3 min intervals the number of feeding group members (Van Belle et al., 2013a).

We manually tagged each tree in which black howlers were observed to engage in at least one feeding bout, which diameter at breast height (DBH) was above 10 cm. For this, we used a biodegradable fishnet and ribbon marked with a specific code for each study group followed by a numeric sequence. After tagging a tree, we recorded its GPS location, we measured its DBH and we estimated its height. In addition, we

identified the species of the tree and estimated its phenological state (see below). If we were not able to identify the tree at species level in the field, we took pictures and gathered leaves and fruit samples to discuss it with an expert botanist (Dr Álvaro Campos, Universidad Nacional Autónoma de Mexico).

In addition, we used feeding bout data to identify the top 10 food species fed by black howlers at PNP (*Poulsemia armata*, *Ficus spp.* ($N_{species}$=7), *Brosimum alicastrum*, and *Acacia glomerosa;* Van Belle, unpubl. data). Subsequently, we located and marked all individual trees with a DBH larger than 10 cm from these species throughout the home ranges of the study groups (Balam: N=137; Motiepa: N=220; Naha: N=213; Pakal: N=227; Unites: N=134). To correct for inaccuracies of the recorded coordinates for each feeding tree, we measured the distance and angle among recorded trees using a tape and a compass. Subsequently, we corrected the recorded GPS locations in QGIS 3.0 and ArcMap 10.4 using such metrics. Every time the focal group was observed feeding in a previously recorded feeding tree, we recorded in our database the code of the tree instead of marking it again.

Finally, detailed behaviour related to black howlers' loud calling were collected in parallel to the present study: Dr Sarie Van Belle and Elsa Barrios recorded the start and end times of all loud calls emitted by the focal group together with its geographic locations. They categorised each loud calling bout according to Van Belle et al., (2013b) as: 1) intergroup encounters (hereafter IGE), whenever a neighbouring group was within visual contact of the focal group during the loud call emission; 2) response to loud calling bouts, following nearby calls from neighbouring groups without visual contact; and, 3) spontaneous loud calling bouts, whenever loud calls occurred in the absence of discernible external stimulus. Even though this information was not collected

specifically for the purposes of the present thesis, I used data regarding loud calling behaviour in the last research chapter (Chapter 6).

2.4.2 Tracking data

We recorded a travel bout whenever two or more group members moved into a neighbouring tree or other part of the forest until at least two members of the group engaged in an activity different from that in the original tree (i.e., loud calling, resting or foraging; Van Belle et al., 2013a). During travel bouts, we collected GPS locations every 20 m at the estimated centre of the group (device: GPS Garmin 64X). Black howlers are highly cohesive species that typically travel in a line formation through the same sequences of trees (Carpenter, 1934). Thus, recording the estimated centre of the group is a standard practice in howlers studies (Hopkins, 2011). If howlers used an already marked tree to travel, we used the coordinates that we had previously recorded instead of recording the GPS location again. We estimated the goal of a travel bout as the predominant behaviour shown by two or more individuals upon arrival (Van Belle et al., 2013a). In addition, we recorded the departure and arrival time and direction using a chronometer and a compass respectively.

We estimated the mean GPS error by recording GPS coordinates in ten well-known locations within the study site (e.g., parking lot, entrance to PNP, specific Mayan ruins) in more than five different days under different weather conditions. Subsequently, we average the distance among all locations collected at the same spot. The resulting mean GPS error was 6.55 ± SD 2.27 m.

2.4.3 Digital Elevation Model

Barnhart, (2001) recorded the topographic characteristics of the landscape during the archaeological mapping of the Mayan city of Palenque using a *GTS-211D* total station (Topcon Corporation) by bouncing light off a movable prism. I adjusted the AUTOCAD version of such archaeological map into updated GIS formats in order to incorporate the attributes of the landscape into the analyses. Thus, I georeferenced the TIN (i.e., a vector-based digital geographic layer representing the surface morphology) version of the map using 15 salient features of the landscape (e.g., roads, Mayan ruins) visible both on the archaeological map and freely available satellite layers. Subsequently, I triangulated the three-dimensional locations into ArcMap 10.4 to create a Digital Elevation Model (DEM; Nelson et al., 2009). I overlaid a grid layer of 10x10 m^2 quadrats and extracted the values for slope and elevation values within each quadrat using the Spatial Analysist tool from ArcMap 10.4. I calculated slope values as the coefficient between the highest and lowest point within each cell and elevation as the absolute height at the centre of the cell (Warren et al., 2004).

I marked the edges of canopy gaps in the field using a GPS device and corrected them using satellite imagery. I used remotely sensed images on land cover from NASA's Landsat 8 satellite for this purpose (Roy et al., 2014). Subsequently, I created a buffer of 25 m from the centre of each quadrat and calculated the percentage overlap between such a buffer and the recorded canopy gaps (Fig. 2.3).

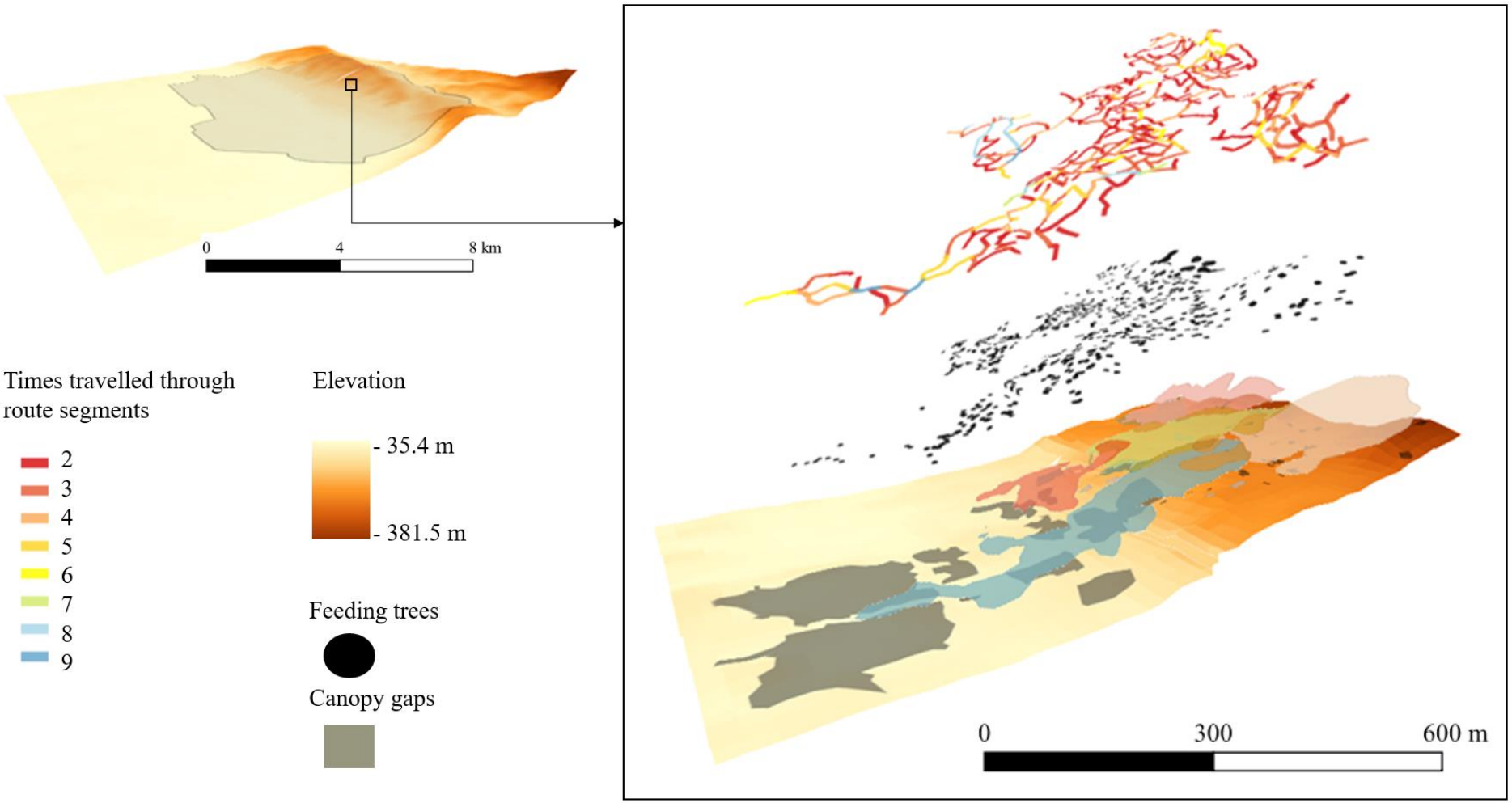


Figure 2. 3 Three-dimensional representation of PNP with its natural elevations (dark orange), black howlers' home ranges (Motiepa: red; Naha: blue; Pakal: green; Unites: pink; and, Balam: brown), all marked food trees (black points), and route networks of the studied population based on data from September 2016 until August 2017.

2.4.4 Remote sensing

I extracted remotely sensed information on plant phenology from NASA's satellites TERRA and Landsat 8. TERRA and Landsat 8 have been recording snapshots around the globe using moderate resolution imaging spectrometer (MODIS) since 1999 and 2013 respectively (Roy et al., 2014). TERRA takes global snapshots every month and corrects the image against potential obstructions due to clouds at a resolution of 250 m^2 per pixel. Landsat 8 takes snapshots every two weeks at a resolution of 30 m^2. For both set of images, I estimated plant phenological activity calculating the Normalized Diversity Vegetation Index (hereafter NDVI) as the resultant coefficient between earth surface reflectance patterns in the red and near-infrared regions of the electromagnetic spectrum (Tucker et al., 2005; Willems et al., 2009). NDVI is a measure of photosynthetic activity which has been used to study vegetation quality, phenology and primary productivity in savannahs (Willems et al., 2009), littoral forests (Donati et al., 2020) and tropical forests (Pettorelli et al., 2011). I used such values to estimate the availability of food resources within PNP and, specifically, within the estimated home ranges of the study groups throughout the study period (Tian et al., 2015). Data were retrieved from the Earth Resources Observation System web-site (http://eros.usgs.gov/products/satellite.html).

2.4.5 Phenological observations

Sarie Van Belle estimated plant productivity across the study period by establishing a phenological trail (*ca*. 10 km) that crossed the entire area used by the five study groups between September 2016 and January 2019. Sarie Van Belle monitored all selected trees ($N = 968$ individual trees; 60 tree species) estimating the abundance of main feeding items (i.e., mature fruits, young fruits, mature leaves, young, leaves,

flowers) every three weeks over a four-day period. Occasionally, Elsa Barrios observed the phenology of trees along the transect. For both observers, we verified that the data was consistent by running an interobserver reliability test. The estimations of abundance indicated the observed quantity of each item in the crown of the tree as follows: 0 = absent, 1 = 1–25%, 2 = 26–50%, 3 = 51 – 75%, and 4 = 76 – 100% (Van Belle & Estrada, 2019). For instance, if the total combination of the percentages of mature and young leaves was 100%, the tree was completely covered in leaves.

2.5 Data storage, management and statistical analyses

We transferred long term behavioural data from HanDBase to Microsoft Access on a weekly basis and checked the occurrence of typos and inaccuracies once a week by having a group meeting and discussing the data together. Similarly, we transferred tracking data from both GPS-devices every week to MapSource to convert GPX data into text files. Subsequently, we transferred weekly tracking data into Microsoft Access and plotted it into QGIS 3.0 and ArcMap 10.4 to correct for potential errors.

I conducted all statistical analyses using the R-project software 3.5.2 (R Core Team, 2018). I used a range of statistical methods that encompassed non-parametric statistics, analyses of variance (ANOVAs) and linear regression models. I ran all linear regression models using the "lmer" and "glmer" functions of the *lme4* package 1.1-21 (Bates et al., 2014) and *glmmTMB* 0.2.2.9 (Brooks et al., 2017). I verified that the residuals of the models were normally and homogeneously distributed by visually inspecting qq-plots and plotting them against fitted values. I also tested for multicollinearity by inspecting variance inflation factors using the "vif" function from the *car* package (Fox & Weisberg, 2011). Similarly, I assessed the stability of the

GLMMs by comparing the estimates derived from a model based on all data with those obtained from models based on subsets, which excluded levels of the random effects one at a time. No model assumptions were violated. In all cases, I compared the full model to a corresponding null model (with only random and control variables) using likelihood-ratio tests ("anova" function set to "Chisq"). When an interaction term had no significant effect, I ran a reduced model including only the main effects. Finally, if the likelihood-ratio test for full and null model comparison was significant, I inspected the significance of each predictor variable using likelihood- ratio tests comparing full models with reduced models without the variables of interest, using the "drop1" function (Barr et al., 2013).

In addition, I estimated the home range of the study groups using the R package *adehabitatHR* 0.4.15 and the Kernel Density Estimation (KDE) method with the GPS locations of the group scan samples (Calenge, 2006). I defined a group's home range as the 95% KDE isopleth and core area as the 50% KDE isopleth (Van Belle et al., 2013a). I specify further details on the statistical models and tests, as well as the R packages used to analyse my research questions within the data analysis section in each chapter.

Chapter 3: Cognitive maps in a Neotropical primate (*Alouatta pigra*)

3.1 Introduction

Living in a tropical forest involves coping with a complex environment characterised by a highly variable spatial and temporal distribution of feeding sources (van Schaik et al., 1993, Chapman et al., 2003; Janmaat et al., 2016). The ability of integrate, recall and constantly update information regarding the location of food sources by an animal across its home range might strongly enhance its ranging performance and ultimately benefit its fitness (Zuberbhüler & Janmaat, 2010). The cognitive effort employed to encode spatial information has been hypothesised to be analogous to the internal representation that animals are able to generate, and potentially determines the spatial strategy that will be used to navigate (Byrne, 1979; Garber, 2000).

In animals, spatial information has been described to be encoded in cognitive maps, which can be structured either based on routes or coordinates depending on the cognitive capacity of the species (Tolman, 1948; Garber, 2000; but see Warren, 2019). Byrne (2000) explains that route based cognitive maps – or network maps – contain only the minimal directional information needed to choose between habitual routes. Individuals learn several interconnecting routes in a graph-like manner in which they remember the topological relations among specific locations as strings but lacks attribute information about the routes themselves (Byrne, 2000; Warren, 2019). Even though route navigation has been reported in a wide variety of animal species (insects, Wehner & Wehner, 1990; birds, Guilford & Biro, 2014; mammals, Newmark & Rickart, 2012; Trapanese, 2019), it likely constrains the flexibility of animals' movement and decision making (Di Fiore & Suarez, 2007). Movement trajectories

might be determined by the shape of such a route network and not by the most efficient path connecting the starting location with the goal (Poucet, 1993; Bennet, 1996; Valero & Byrne, 2007). Consequently, limited cognitive skills might lead to potentially secure but inefficient navigation (Trapanese et al., 2019).

Animals navigating on the basis of a coordinate based map – also called *vectorial maps* (Byrne 2000) and *metric maps* (Dyer, 2000) – are hypothesised to compute distances and angles based on features of the landscape generating an Euclidean representation of its habitat (Tolman, 1948; McNaughton et al., 2006). Under this scenario, animals would be able to navigate in a highly flexible manner in space, engaging in novel paths when needed (Poucet, 1993). In terms of cognitive effort, route based maps only require an animal to remember a sequence of landmarks and intersections while a coordinate based maps might require the storage and processing of multiple directions, distances and goals in a highly accurate fashion (Norman & Boesch, 2009; Trapanese et al., 2019). Even though the mere existence of coordinate based maps in animals and humans has been debated during the last decades (Tolman, 1948; Poucet, 1993; Garber, 2000; Janson, 2014; Warren, 2019), evidence describing the Euclidean abilities of some species has been reported in the literature (e.g., honey-bees, *Apis melifera*, Cheeseman et al., 2014; African elephants, *Laxodonta africana*, Presotto et al., 2019; black capuchin monkeys, Presotto & Izar, 2010). A combination of both route and coordinate cognitive maps has also been suggested in some species, where animals might adjust their navigation strategy under different physical and ecological conditions (Presotto & Izar, 2010; Presotto et al., 2019; Porter & Garber, 2013).

Among the criticism faced by research on foraging cognition in wild animal populations is the lack of a null models or controls (Shettleworth, 2010). Experimental research typically designs control settings against which to test hypotheses associated

with cognitive representation (Janson & Byrne, 2007; Janson, 2019). Although we will never be able to account for the complete set of events experienced by wild populations that can condition their movement patterns (Janson, 2019), there is potential for using random-walk movement as a control (Garber & Hannon, 1993; Gautestad, 2011). For instance, computationally generated patterns of random movement have revealed the importance of memory in migratory routes of terrestrial ungulates in Botswana (zebras, *Equus burchelli antiquorum*, Bracis & Mueller, 2017) and home range site fidelity behaviour of cervids in Southern Norway (red deers, *Cervus elaphus*, Gautestad et al., 2013). Suarez et al., (2014) went a step further and simulated random movement within a previously detected route network in spider monkeys (*Ateles belzebuth*) at Yasuní National Park, Ecuador, instead of using the entire home range. Simulated agents were outperformed by spider monkeys: observed spider monkeys travelled shorter and straighter paths than simulated agents highlighting the value of spatiotemporal information of food resources during route based navigation (Suarez et al., 2014). Further comparisons between simulated and observed movement patterns can validate previous findings by not only examining specific movement measures but also statistically compare them against potential controls.

Identifying an animal's ability to compute novel-short cuts between known locations is the primary diagnostic of the presence of Euclidean mental representations (Byrne, 2000). In wild populations, it is only possible to determine such ability by tracking their movements since birth (Harten et al., 2020), following reintroduced populations since release (Ranc et al., 2020) or running experiments in provisioned platforms (Janson, 2019). Since we collected non-invasive, naturalistic observations in already settled wild animal groups, we attempted to describe the cognitive maps by the study species combining a set of indirect evidence extracted from their ranging patterns.

To obtain each of the evidence mentioned in the text below, we tested a series of cognitive hypothesis against simulated random movement patterns that mimicked the characteristics of observed movement (Suarez et al., 2014).

First, describing the tendency of the study species to travel through the same areas repeatedly will be indicative of relying into a route based cognitive map to navigate (Preotto & Izar, 2010; Porter et al. 2018; Presotto et al., 2019). For instance, Di Fiore & Suarez (2007) overlaid 8-year tracking data on spider monkeys (*Ateles belzemuth*) and woolly monkeys (*Lagothrix poeppigii*) inhabiting the Amazonian Ecuador. These sympatric species were shown to not only systematically reuse the same routes to travel to distant feeding sites but also to use the same routes with each other across study years (Di Fiore & Suarez, 2007). Similarly, other arboreal animals were shown to repeatedly overlap travelling paths across multiple months or even years (proboscis monkeys, *Nasalis larvatus*, Boonratana, 2000; Wedelli's saddleback tamarins, *Saguinus fuscicollis weddelli*, Porter & Garber, 2013; bearded sakis, *Chiropotes sagulatus*, Gregory et al., 2014). A similar pattern was found in African elephants (*Loxodonta africana*) in Kruger National Park, South Africa, which typically overlapped their paths but only in the periphery of their home range (Presotto et al., 2019). Black capuchins showed the opposite pattern in Carlos Botelho State Park, Brazil, increasing the overlap of travelling paths but only in the core are (Presotto & Izar, 2010). To date, chimpanzees in Taï Forest, Ivory Coast, have been the only species that showed almost no overlap among their travel paths suggesting the use of a coordinate based map (Normand & Boesch, 2009; Porter et al., 2020).

Navigating using route based cognitive maps has been hypothesised to constrain an animal's ability to go back to specific, biologically meaningful locations in a flexible manner (Noser & Byrne, 2007a). Contrary to coordinate based navigation, travelling

through routes implies following specific sequences of trees or landmarks in order to reach such locations limiting the number of options to arrive and depart from. Thus, an animal's ability to reach relevant feeding sites from multiple different directions or paths can be used as an evidence for determining their cognitive map (Poucet, 1993). For instance, Urbani (2009) showed that white-faced capuchins (*Cebus capucinus*) approached revisited feeding sites using 11.7 different paths, of which only 4 were used more than once. The elevated number of different directions used to revisit feeding sites complemented the monkeys' tendency to overlap travel paths in La Suerte Biological Station, Costa Rica (Urbani, 2009). White-faced capuchins were suggested to be using a coordinate based map in small-scale movements, which enhanced their flexibility when approaching feeding sites, together with a large-scale route based cognitive map used to navigate among food patches (Urbani, 2009; also reported in tamarins, Garber & Porter, 2014; and Hamadryas baboons, Schreier & Grove, 2014). In close proximity to foraging goals, the scent and visibility of feeding items will likely drive the movement decisions of wild animals instead of mental representations (Janmaat et al. 2013). Combining evidence will, therefore, provide a better picture of an animal's cognitive skills and avoid biases due to sensory cues. Yet, not all animals show revisiting patterns to biologically meaningful locations (Berger-Tal & Bar-David, 2015), which may as well occur over prolonged periods of time (English et al., 2014). Thus, each study exploring the mental representations of each species needs to be tailored to biology and sensorial adaptations of the study model (Bracis et al., 2018).

Lastly, route based cognitive maps have been described to be structured not only by habitual route segments but with nodes as well, which are locations were habitual routes intersect and directional decisions are made based on perceived landmarks from the landscape (Byrne, 2000; Presotto et al., 2018). For arboreal animals, nodes were

described to concur with emergent trees that provided a better view above the canopy (Milton, 1981; Pereira, 2008). Terrestrial animals were described to potentially rely on landscape features (i.e., mountains, cliffs) that were visible from further away distances as landmarks to re-orientate their direction (De Raad & Hill, 2019; Noser & Byrne, 2014). Presotto et al., (2018) found that the semi-terrestrial tufted capuchin monkeys (*Sapajus libidinosus*) recalled intersections in their route network to habitually engage on directional changes. Such intersections were located on "*steeper ridges with unblocked visual access over long distances*" (p.403, Presotto et al., 2018). Hence, nodes likely benefit route based navigation by introducing novel environmental information in the movement decision making of animals (Suarez, 2003). In addition, navigation efficiency throughout a route network will depend on the structure of the route network itself (Bast et al., 2016). The higher the number of nodes and connections within a network, the more cognitive power will be needed to plan an efficient trip (Gallotti et al., 2016). Also, further parameters have been argued to influence the efficiency of route networks such as degree of centrality (i.e., relative number of connections of each node in relation to the network) or modularity (i.e., how similar interconnected nodes are creating subdivisions within a network; Schieber et al., 2017). Therefore, determining the presence of nodes is a first step to understand the use of cognitive maps in animals but examining the structure of the network itself through its nodes and connections will shed light on the animal's cognitive skills and efficient navigation.

Each of the types of evidence mentioned above – path overlap, revisiting number of paths and use of nodes – do not necessarily exclude a Euclidean map-like awareness on its own but combine into a single framework (Fig., 3.1; de Raad & Hill 2019). In addition, by examining these features together, results that *a priori* would

have been contradictory have helped in understanding the combination of ranging strategies in some species (Urbani, 2009; Presotto & Izar, 2010; Porter & Garber, 2014). Integrating each attribute will provide a more accurate framework and will shed light on the evolutionary processes and ecological pressures that shaped primate navigation (Garber & Dolins, 2014).

To date, contradictory findings have been reported in the literature since Milton (1981, p. 540) first stated that "*howler monkeys repeatedly used a set of arboreal pathways to move between certain feeding and resting trees*". Nicaraguan mantled howler monkeys (*Alouatta palliata*) have exhibited the ability to reach the same feeding site from different locations (Garber & Jelinek, 2006). Garber & Jelinek, (2006) also

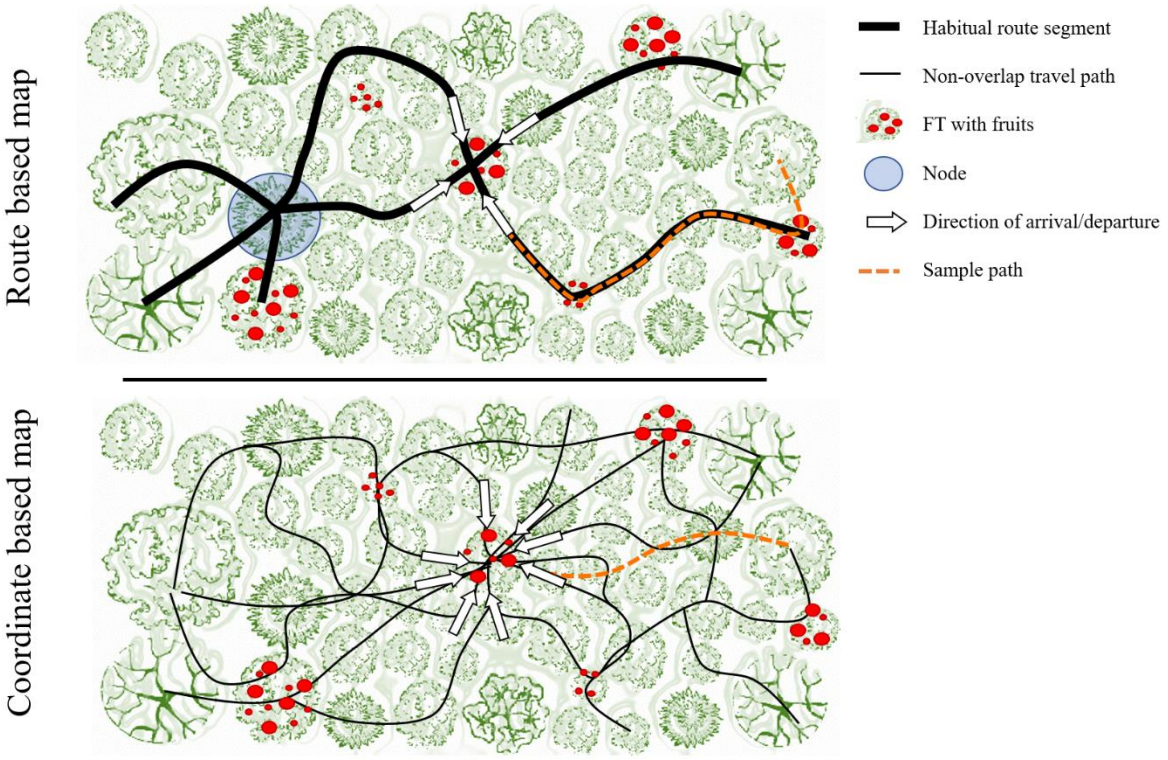


Figure 3. 1 Illustration of the characteristics associated with route and coordinate based cognitive maps regarding: (1) path overlap; (2) number of directions used to approach revisited trees; and, (3) presence of nodes to take directional decisions. The dashed orange line illustrates a sample path traveling in between the same two places using a coordinate based cognitive map (above, performing a short cut) and a route based cognitive map (below, relying on habitual routes).

showed that routes used by mantled howler monkeys were shorter when reusing the same tree sequences, which also suggests the potential use of a coordinate based map. Contrary to this, Panamanian howler monkeys in Barro Colorado Island, Costa Rica, were shown to increasingly overlap their travel paths when moving towards different feeding goals (Hopkins, 2011; 2013). Similarly, brown howler monkeys (*A. guariba clamitans*) also tended to travel using the same arboreal pathways and emergent trees as nodes (Pereira, 2008). This variation in navigation strategies of such closely related species might be explained by either interspecific cognitive divergence or other cofounding factors (i.e., landscape constraints, dietary differences, seasonality; Fortes et al., 2015). Therefore, further research combining all evidence associated with different cognitive maps into a single framework for each species in their natural habitat is the most optimal approach to elucidate the cognitive evolution within *Alouatta* and among other primate species (Tujague & Janson, 2018; Trepanese et al., 2019).

Here, I aimed to examine in detail the characteristics associated with using cognitive maps in wild black howlers at PNP. First, I simulated correlated random-walk within the home ranges of the study groups in order to have a control against which to compare evidence extracted from observed movement patterns (Hopkins, 2016). Second, I determined the tendency for black howlers to: (1) overlap their travelling paths; (2) approach and depart from revisited feeding site following the same directions; and (3) use nodes to re-orientate their movements (see Table 3.1 for hypotheses). I expected that black howlers will consistently use either a route or a coordinate based map to navigate throughout their home range.

Table 3. 1 Summary of predictions related to cognitive maps for the random-walk movement and observed movement patterns.

Evidence	Random movement	Route based map	Coordinate based map
Tendency to overlap travelling paths into habitual routes	Sporadically	High	Low
Tendency to arrive and depart from revisited locations through the same directions	Low	High	Low
Tendency to use nodes to re-orientate	None	High	None

3.2 Methods

3.2.1 Data collection

See section 2.1 – 2.4.

3.2.2 Data analyses

I compared black howlers' tendency to overlap travel paths with simulated random-walk paths generated within the estimated home ranges (Suarez et al., 2014). First, I used the packages "adehabitatLT" 0.3.24 (Calenge, 2006), "SiMRiv" 1.0.3 (Quaglietta & Porto, 2019) and "sf" 0.7–6 (Pebesma et al., 2019) in R6.0 to simulate correlated random-walks. Correlated random-walk assumes an independent distributions of step lengths and turning angles in two different states describing an animal's path based on real data (Kareiva & Shigesada, 1983; see Appendix I). Each state draws a set of movements that are considered correlated with each other since the move angles are not distributed uniformly around the circle as in pure random-walk models (Bergman et al., 2000). Since we collected data on the same group during four consecutive days a week, ranging behaviour was spatially autocorrelated within weekly sampled units (Cushman, 2010). To mimic the characteristics of the recorded data, I ran as many simulations within each home range as weekly sampled units controlling for distance travelled (Motiepa = 15; Naha = 17; Pakal = 15; Unites = 13). I ran each simulation at a resolution twenty times higher than the original data to reproduce fine-scale movement steps with the "adjustModel" function of the package "SiMRiv". I down-sampled the output to the reals data's frequency and controlled for the number of metres simulated to match the length of the original data (Fig. 3.2). Since the aim of this chapter is to find the most parsimonious explanation for the navigation strategy of black howler monkeys, I decided to set the background resistance to 100% so that the code

assumed non-resistance within black howlers' home ranges and total resistance outside of the home range (Seidel et al., 2018). For a more detailed description on how landscape features influence the formation of routes in heterogeneous landscapes, please see next chapter.

Second, I generated the route network used by both the study groups and the simulated random-walk agents. I overlaid all daily travel paths recorded during the same week per group onto a raster map of the area and checked their concordance (Di Fiore & Suarez, 2007). Whenever a daily path fell within a 10 m buffer of another daily path of that week for at least 15 m without deviating more than 45° from the other path, I considered it as the same travel segment (Presotto et al., 2018). I selected these parameters in order to be consistent with previous research and to control for GPS accuracy and travel directionality (Di Fiore & Suarez, 2007; Presotto & Izar, 2010; Garber & Porter, 2014; Bebko, 2018). Food resources in rainforests can occur for a short period in the same location within the same week (Janmaat et al., 2016), which can lead to an overestimation of the frequency of used routes (Presotto & Izar, 2010). Hence, I first constructed "weekly paths" including only unique daily paths of each sampled week to avoid a bias towards re-used route segments due to short revisiting intervals to certain feeding trees (FTs) within that same week. Each group's weekly paths were overlaid on top of each other and I repeated the same procedure as described above to determine across how many weeks route segments were used (Presotto et al., 2019). I defined the habitual route network of each group as path segments used during at least two separate observation weeks. For the simulated movement, I followed the same protocol by describing path overlap within sampling units to generate simulated-weekly paths and, subsequently, determining overlapment among all simulated weekly paths per group.

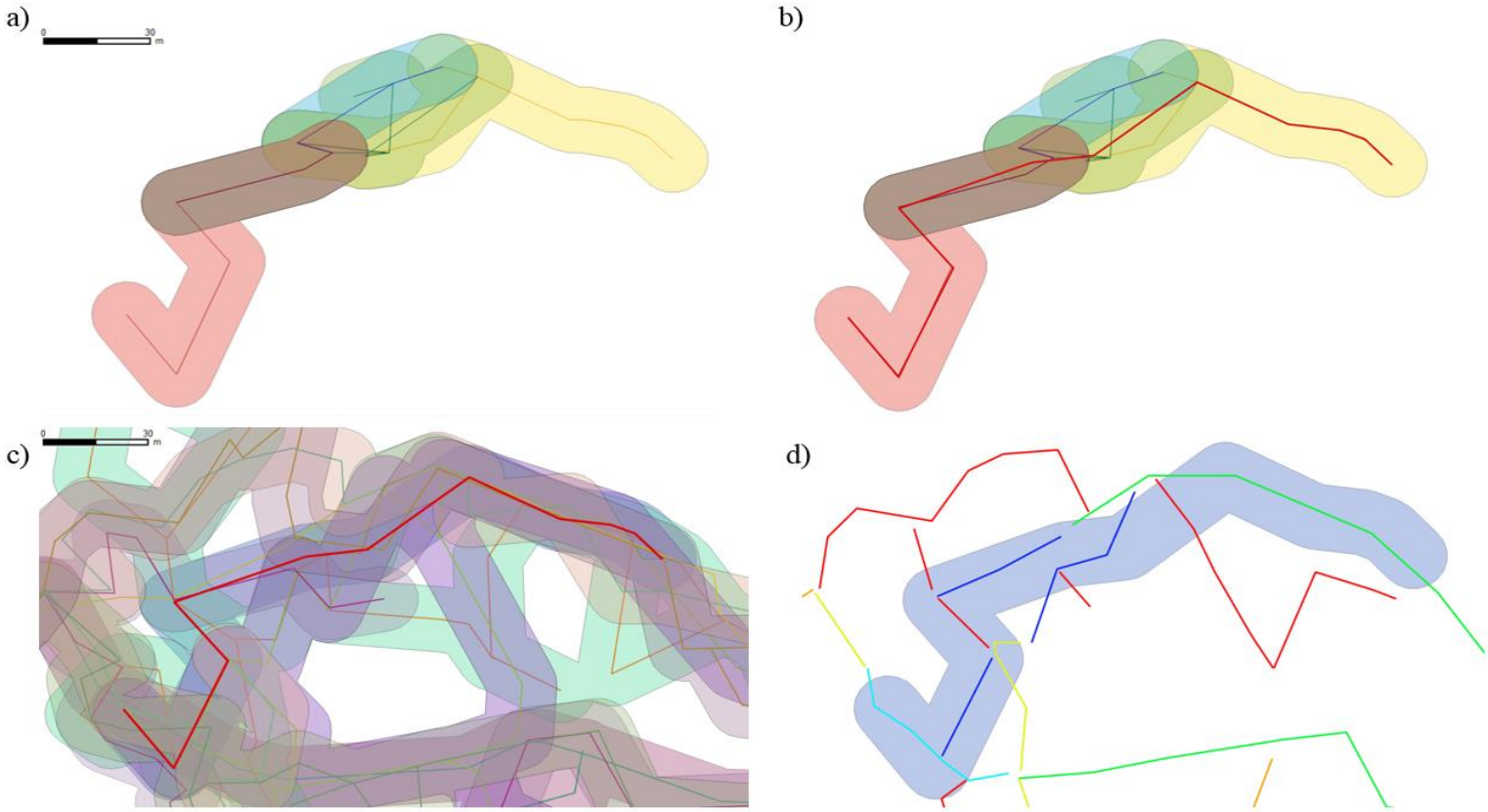


Figure 3. 2 Illustrative example on how the route network is described based on the accumulative overlap of travel bouts: a) daily travel paths performed within the same week (each colour represents a different day) with a buffer area of 10 metres on each side; darker areas represent overlapping segments of the daily travel paths; b) A weekly path is traced on top of all single used and repeated used travelling segments in order to discard backtracking; c) All weekly paths are overlapped among each other with a buffer of 10 metres on each side; and d) Route segments repeatedly used: twice=*red*; three times = *green*; four times= *yellow*; nine times=*cyan*.

Once I had generated all route networks, I tested whether the overall distance travelled by black howlers within route networks was higher than simulated agents. For this, I calculated and compared the total number of metres travelled within and outside a 10 m buffer from the centre of the route segments used at least twice. In addition, I tested whether the frequency of travelling through habitual route segments was higher for black howlers or simulated agents. I calculated habitual route segment travelling frequency as follows:

$$Frequency = \sum_{times\ used}^{Group} \frac{Length\ segment}{(total\ distance\ travelled/N_{days})}$$

where the coefficient between the distance of the weekly travel paths that fell within that route segment and the number of sampling days was divided by the length of the habitual route segment. I calculated the frequency of use for route segments used between two and nine times separately for each group in both observed and simulated movement patterns.

I then compared whether black howlers tended to approach and depart to revisit FTs using the same routes (i.e., through the same direction) and whether the number of different routes used differed from simulated movement patterns. For this, I assumed that black howlers were using the same route when the observed arrival and departure angle did not differ more than 20º from the directions of previous visits to that same FT, while angles differing more than 20º were considered as different routes (Urbani, 2009; Fig. 3.3). I calculated the total number of routes used to reach FTs that were visited, at least, five times during the data collection and divided it by the total number of visits to these FTs.

Because simulated random-walk agents were not revisiting FTs, I used the R-package "*recurse*" (Bracis et al., 2018) to identify highly revisited locations within the home range that could act as hypothetical feeding sites. The "*recurse*" package works by generating a circle of a specific radius and moving it along the trajectory. At each point, the number of trajectory segments entering and exiting the circle is counted to determine the number of revisitations (Bracis et al., 2018). In order to mimic the characteristics of black howlers, I selected a radius of 35 m based on the estimated visual window of black howlers in rainforests (Milton, 1981; Appendix I. Fig. 3).

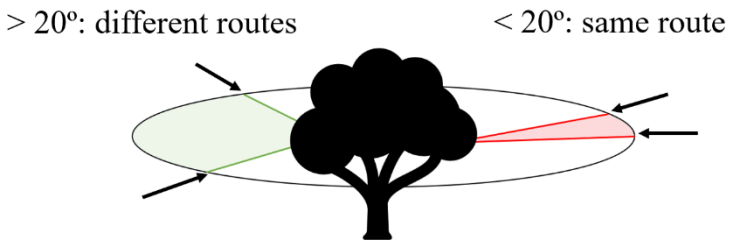


Figure 3. 3 Criteria used to determine whether the observed group of black howlers was approaching and/or departing FTs through the same route (directions that were within 20º of each other, red area) or different routes (directions that further than 20º from each other, green area).

Subsequently, I randomly selected as many locations as revisited FTs in each home range that were within the pool of locations that were visited at least five times by the simulated agents. Finally, I calculated the number of different directions used to reach these locations following the same protocol as described to revisited FTs. I compared both the accumulated number of directions and the travelling frequency through each direction to approach and depart from revisited locations by black howlers and simulated agents.

Additionally, I examined the presence of nodes in both set of networks. I defined "node" as a location in which two or more habitual route segments intercepted each other followed by at least one change in direction larger than 45º within the next 15 m from the intersection (Presotto et al., 2018; Fig. 3.4). Subsequently, I described the connections among all nodes (hereafter called "edges") of the same network and the number of times that such connection was used to travel. I constructed a correlation matrix for each network describing the connections among all nodes and calculated a set of global (network level) and local (node level) parameters to compare the properties of both sets of networks (described in Table 3.2). I conducted all network analyses using the R-package "*igraph*" v1.2.4.2.

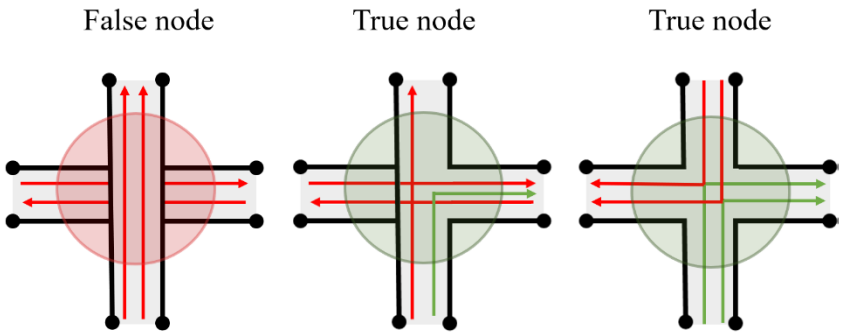


Figure 3. 4 Criteria selected to determine whether the intersection between habitual route segments represents a node.

Table 3. 2 Summary of the parameters examined in the simulate and observed route networks to compare their overall complexity and connectivity (definitions adapted from Gastner & Newman, 2006; Barthélemy, 2011).

Global scale	
Degree	Mean number of edges connecting each node within a network.
Density	Total number of all possible edges among nodes divided by the number of actual edges. The greater the density, the faster information spreads throughout the network.
Diameter	The shortest distance between the two most distant nodes in the network. The larger a network is, the more costly it will be to travel through it.
Clustering	The overall probability for the network to have interconnected nodes. Clustering or transitivity indicates whether the nodes of a network tend to be connected to other specific nodes forming clusters.
Local scale	
Strength	Average number of travelling events that occurred among interconnected nodes. It indicates how involve a node is in the activity of the network.
Average path length	Average number of steps along the shortest paths for all possible pairs of network nodes. It is a measure of the efficiency of travelling within a network.
Closeness	Average of all shortest path lengths from the node to all the other nodes in the network. Closeness indicates the level of centrality of the network.

3.2.4 Statistical analyses

I used a two-tailed Mann-Whitney evaluate whether simulated agents and black howlers overall distance travelled fell more frequently within or outside the route network. Subsequently, I compared simulated and observed movement by fitting two linear mixed models (LMMs) in which the accumulated distance travelled (overlap model 1) and frequency of use for each habitual route segments (overlap model 2) were

the two response variables respectively. For all models performed in this chapter, I used type of movement (i.e., simulated and real) as main predictor and group ID as random effect (overlap model 1: distance travelled ~ Type of movement + (Type of movement | Group ID); overlap model 2: frequency of travelling ~ Type of movement + (Type of movement | Group ID)).

I designed two further LMMs to test whether simulated and observed movement differed in the number of directions used to arrive and depart revisited locations. In the first model (angles model 1), the response variable was the number of different directions followed to reach and depart such revisited FTs. In the second model (angles model 2), I used the frequency in which simulated agents and black howlers used each direction to reach and depart from revisited sites (angles model 1: total number of directions ~ Type of movement + (Type of movement | Group ID); angles model 2: frequency of directions' use ~ Type of movement + (Type of movement | Group ID)).

To test whether simulated agents and black howlers differ in the structure of their route network, I used the R package *igraph* 1.2.4.2 (Csardi & Nepusz, 2006). I did not run statistical tests for the parameters at a global scale (i.e., degree, density, diameter and cluster) because of the reduced sample size of four groups. Instead, I reported the average value for both simulated and observed movement. For parameters at local scale (i.e., strength, average shortest path length, closeness), I ran Student's t tests using each measurement as response variable and type of route network (i.e., simulated, real) as factor.

3.3 Results

Throughout the study period we collected 3104 hours of behavioural observation ($N_{days\ per\ group}$= 59.8±2.17; $N_{hours\ per\ group}$= 620.71±29.58). In all groups the main activity was always resting (59.89%) followed by feeding different food items (17.21%). The time spend on travelling accounted for 8.9% of their total activity budget, followed by moving behaviour within the same tree (5.83%) and loud calling (1.62%). Social interactions and aggressions were highly scarce (3.12% and 0.017% respectively) as shown in previous research at PNP and other field sites (Van Belle et al., 2014; Ostro et al., 1999).

Regarding black howler feeding behaviour, 2969 feeding bout scans were recorded (mean number of food scans per group = 553.8 ± SD 98.5) on 1830 different feeding trees, which lasted a mean of 23 minutes (range: 5 min – 3h 23 minutes). Time spent feeding was mainly focused on young leaves (5.87%) and mature fruits (5.19%), followed by mature leaves (1.85%) and young fruits (1.77%), and finally other food items such us stems, petioles or flowers (<1%).

We recorded a total of 1528 travel bouts from all the observed groups of monkeys, with an average of 305.6 ± 43.9 travel bouts per group (range: 250 – 368 travel bouts per group). On average, the length of an individual travel bout was 65.3 ± 57.53 metres while the daily path length accounted for 365.83 ± 199.16 metres (range: 28.28 – 1022.83 metres). Each daily path length consisted of between 2 to 11 travel bouts. Average home range size was 10.38 ± 3.07 ha and core area size was 2.5 ± 0.65 ha. In addition, home ranges overlapped among them on average 0.91 ± 0.18 ha (1.3 – 2.26%).

Simulated random-walk agents were shown to overlap between 58.05% and 65.15% of the total distance travelled (average simulated route network length: 2.9 km ± SD 0.9) while black howlers overlapped between 83.69% and 92.4% of the total distance travelled (average simulated route network length: 3.5 km ± SD 1.1; Table 3.3). The total distance travelled was significantly longer within than outside the route network for both simulated agents (Mann-Withney U = -1.89, $N_1 = N_2 = 4$, p-value = 0.05 two-tailed) and black howlers (Mann-Withney U = -2.31, $N_1 = N_2 = 4$, p-value = 0.02 two-tailed). In addition, the simulated agents and black howlers did not differ statistically in the total distance travelled within the route network (likelihood ratio test: $\chi^2 = 0.031$, d.f. = 1, p-value = 0.856; Table 3.3; Fig. 3.5).

Table 3. 3 Total travelled distance recorded for simulated agent (simulated movement) and each study group (real movement) outside and within their route network expressed in accumulated number of metres and percentage.

Group	N weeks	Distance travelled outside the route network (m)	Distance travelled within the route network (m)
Simulated movement			
Motiepa	15	2,816.70 (30.71%)	6,355.16 (60.29%)
Naha	17	8,048.79 (40.70%)	8,048.79 (59.30%)
Pakal	15	3,271.46 (34.85%)	9,387.43 (65.15%)
Unites	13	4,276.91 (41.96%)	10,194.02 (58.05%)
Real movement			
Motiepa	15	689.31 (7.59%)	9,084.79 (92.4%)
Naha	17	2,082.21 (9.34%)	22,205.51 (90.66%)
Pakal	15	1,642.17 (16.31%)	10,066.29 (83.69%)
Unites	13	1,659.88 (14.48%)	11,456.33 (85.52%)

Simulated agents typically overlapped paths in two or three occasions while black howlers were shown to overlap paths in nine different non-consecutive weeks (Table 3.4). I found statistical differences in the frequency of travelling through route networks in black howler monkeys in comparison to simulated random-walk agents (likelihood ration test: $\chi^2 = 5.82$, d.f. = 1, p-value = 0.016; Fig 3.5). Black howlers travelled at higher frequencies (mean: 0.6 ± 0.04 day^{-1}) than simulated movement (mean: 0.3 ± 0.02 day^{-1}) likely influenced by the lack of habitual routes used more than five times in the simulated movement patterns (Estimate = -0.023; SE = 0.009; CI_{lower} = -0.042; CI_{upper} = -0.005; p-value = 0.016; Fig. 3.5, see also Fig 3.6a,b).

Table 3. 4 Mean (± SD) distance travelled through habitual route segments and mean (± SD) frequency of use for habitual routes segments travelled between two and nine times during the study period[1].

	Simulated movement		Real movement	
Times used	Habitual route segment length (m)	Frequency of use (day^{-1})	Habitual route segment length (m)	Frequency of use (day^{-1})
Twice	2879.12 ± 879.23	0.04 ± 0.01	3360.88 ± 1293.80	0.03 ± 0.01
Three times	1193.38 ± 595.74	0.05 ± 0.01	1843.71 ± 924.69	0.04 ± 0.01
Four times	280.12 ± 151.12	0.07 ± 0.01	952.58 ± 570.97	0.05 ± 0.02
Five times	61.62 ± 68.87	0.09 ± 0.01	622.61 ± 478.79	0.09 ± 0.02
Six times	5.50 ± 11.00	0.03 ± 0.02	360.01 ± 297.20	0.08 ± 0.06
Seven times	0.00 ± 0.00	0.00 ± 0.00	210.69 ± 256.19	0.04 ± 0.06
Eight times	0.00 ± 0.00	0.00 ± 0.00	179.94 ± 255.40	0.06 ± 0.11
Nine times	0.00 ± 0.00	0.00 ± 0.00	42.01 ± 48.61	0.07 ± 0.08

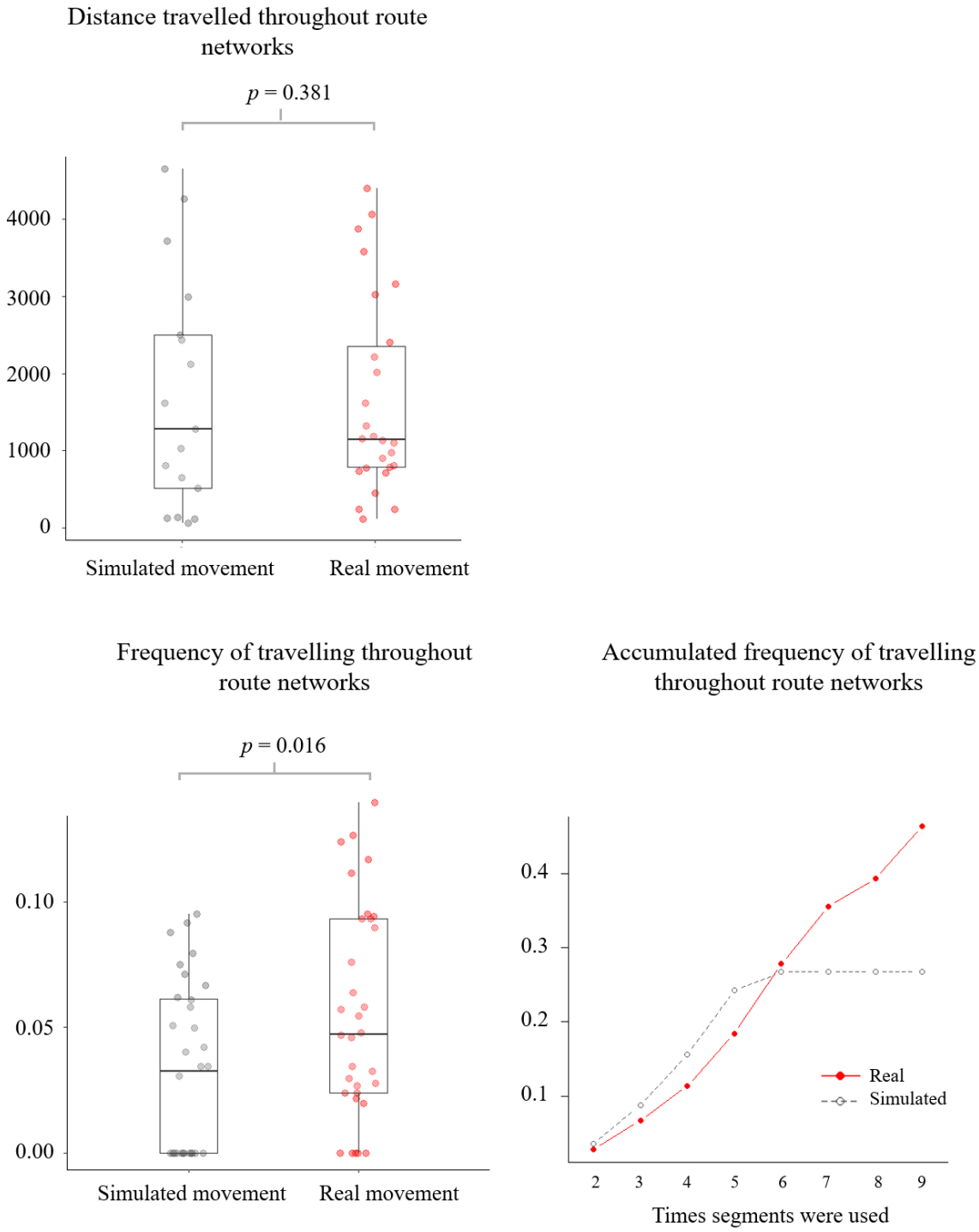


Figure 3. 5 Results of the LMMs testing for differences in the distance travelled within route networks (top) and frequency of travelling throughout route networks (bottom left) in simulated and observed movement patterns. The accumulated frequency of travelling through habitual route segments per times used is shown in the bottom right.

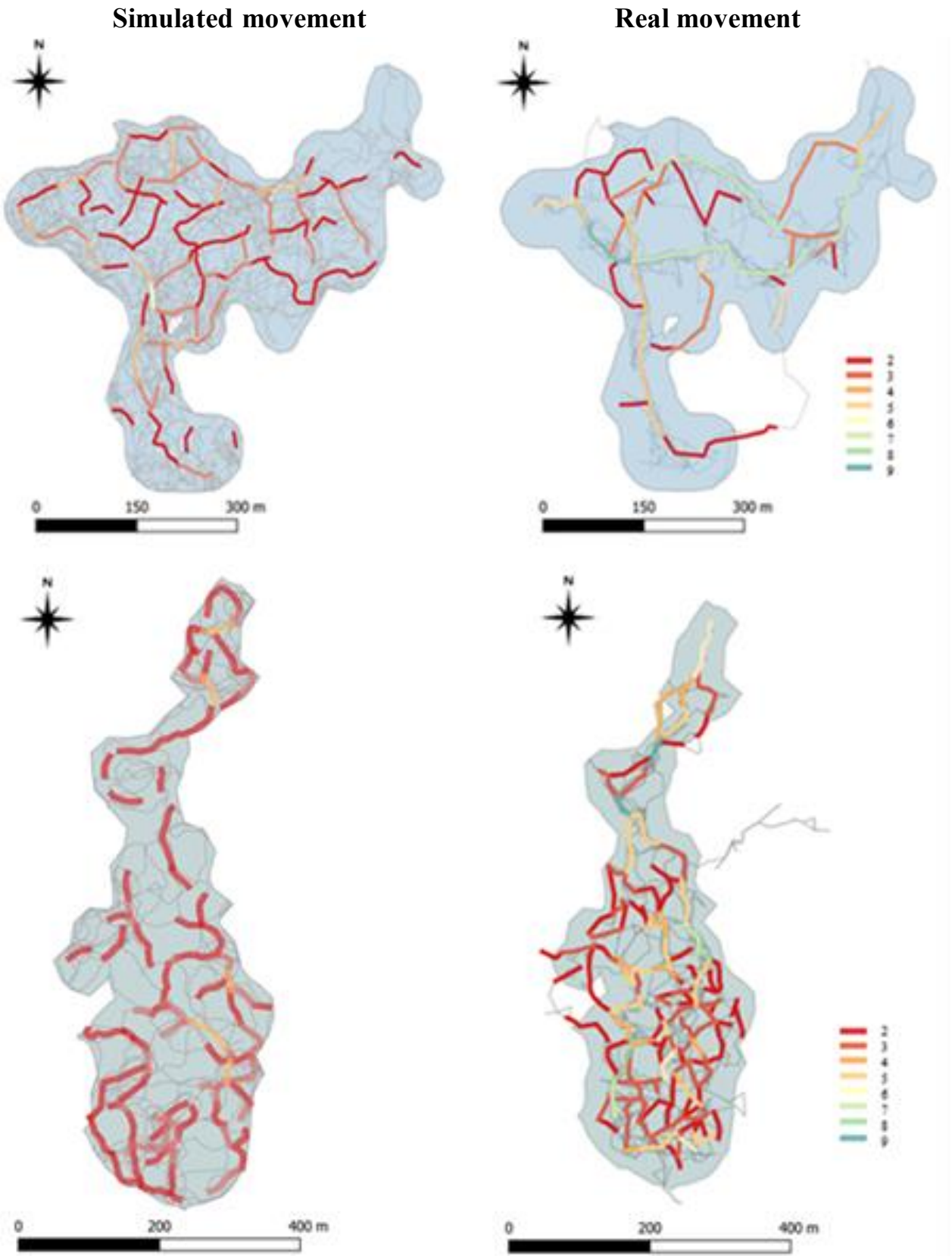


Figure 3. 6a All described habitual route segments for the study groups *Motiepa* (top) and *Naha* bottom) for both real (left) and simulated (right) movement, overlaid on top of all recorded travel bouts (grey lines). The legend illustrates the number of times that each habitual route segment was used during the study period.

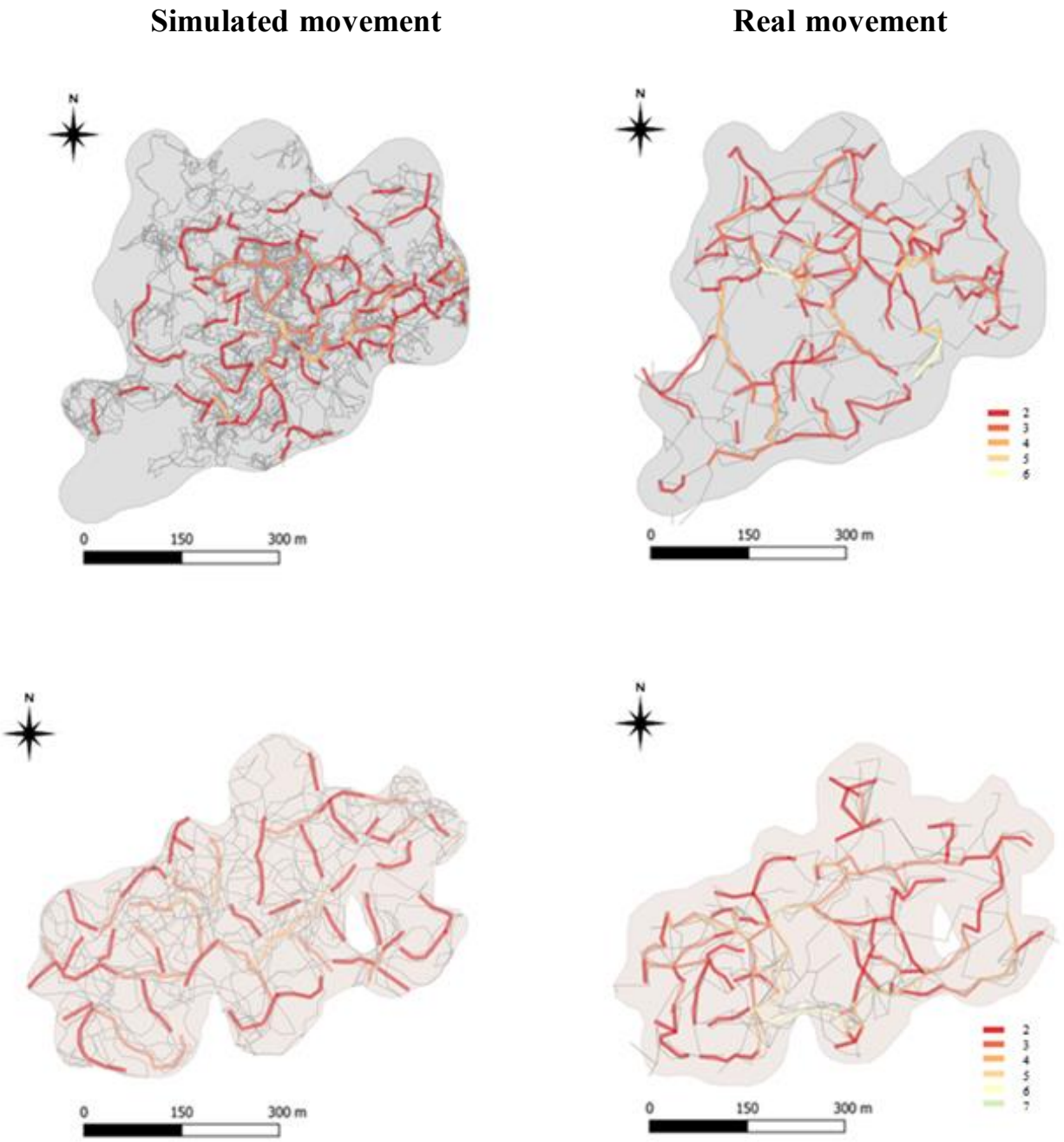


Figure 3. 6b All described habitual route segments for the study groups *Pakal* (top) and *Unites* (bottom) for both real (left) and simulated (right) movement, overlaid on top of all recorded travel bouts (grey lines). The legend illustrates the number of times that each habitual route segment was used during the study period.

Black howlers at PNP showed a tendency to approach and depart from revisited FTs through a lower number of directions in comparison to simulated agents (Table 3.5; Fig. 3.7; likelihood ratio test: $\chi^2 = 8.32$, d.f. = 1, p-value = 0.004). In addition, the frequency in which each direction was used to reach revisited feeding sites differed statistically between real and simulated movement (likelihood ratio test: $\chi^2 = 4.09$, d.f. = 1, p-value = 0.043). Black howlers used the same routes to approach revisited feeding sites more often than simulated movement agents (Estimate = -0.076; SE = 0.025; CI_{lower} = -0.125; CI_{upper} = -0.028; p-value = 0.043; see also Fig. 3.8a,b).

Table 3. 5 Summary of the number of visits, mean number of directions and mean number of times that each direction was used to approach and depart revisited feeding sites.

Group	N visits	Number of unique directions used to reach feeding goals (mean ± SD)	Times each direction was reused to reach feeding goals (mean ± SD)
Simulated movement			
Motiepa	374	8.9 ± 1.7	1.7 ± 0.7
Naha	363	6.6 ± 1.6	1.5 ± 0.3
Pakal	310	9.1 ± 1.8	1.8 ± 0.3
Unites	178	6.8 ± 1.6	1.6 ± 0.3
Real movement			
Motiepa	385	4.6 ± 1.3	1.8 ± 0.5
Naha	319	4.4 ± 1.2	1.7 ± 0.5
Pakal	224	4.4 ± 1.2	1.7 ± 0.5
Unites	181	4.8 ± 2.3	2.1 ± 0.7

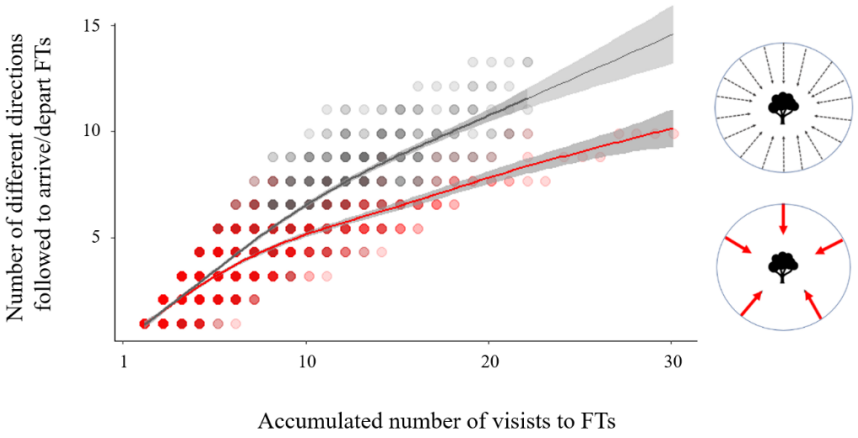


Figure 3. 7 Accumulated number of different directions used to reach and depart feeding sites in relation to the accumulated number of visits to these sites for observed (*red*) and simulated (*grey*) movement.

Simulated movement

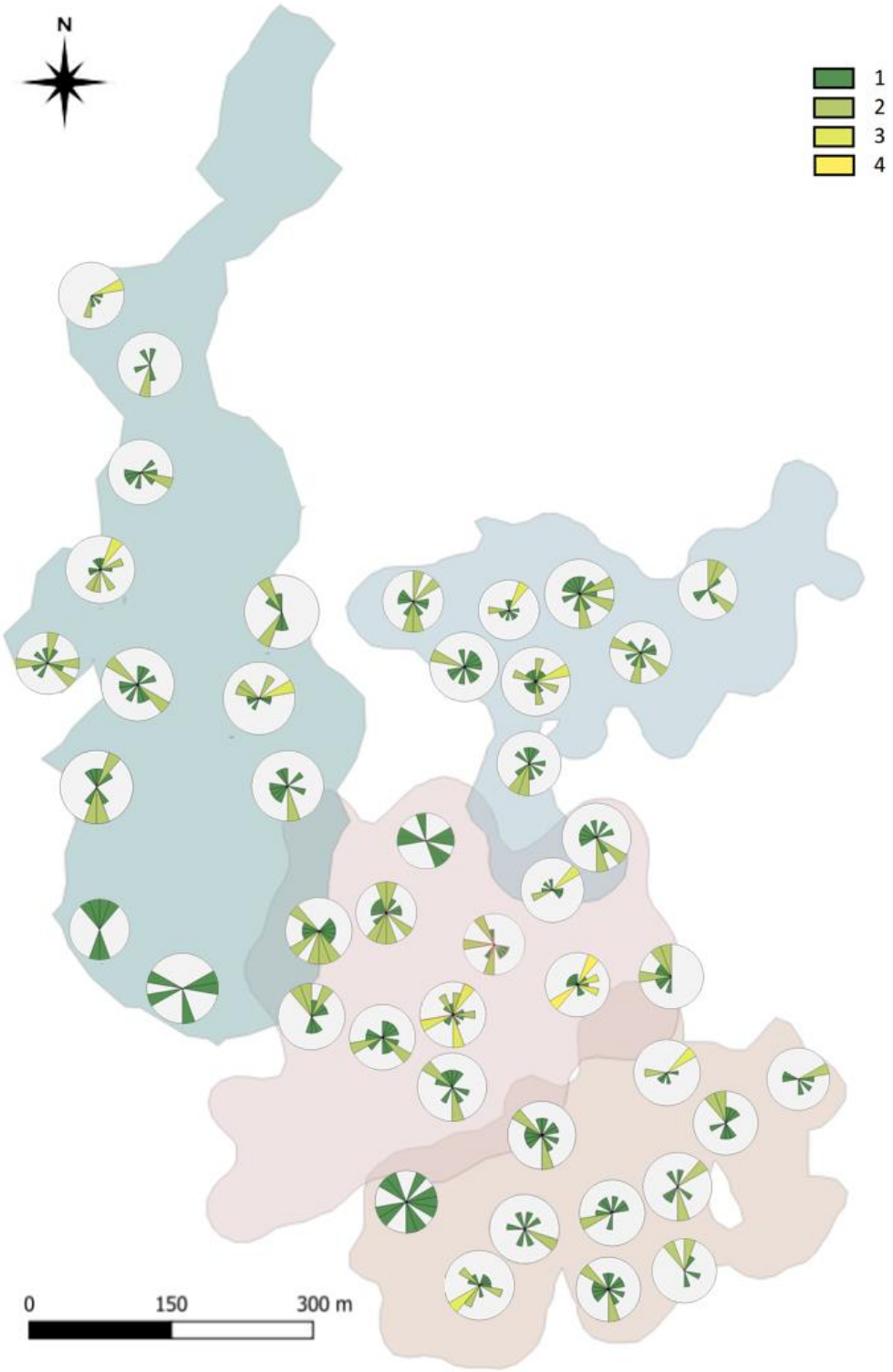


Figure 3. 8a Subset of all described arrival and departure angles combined to reach revisited locations in simulated correlated random-walk movement. The legend illustrates the total number of times that each direction was reused to reach these revisited feeding sites.

Real movement

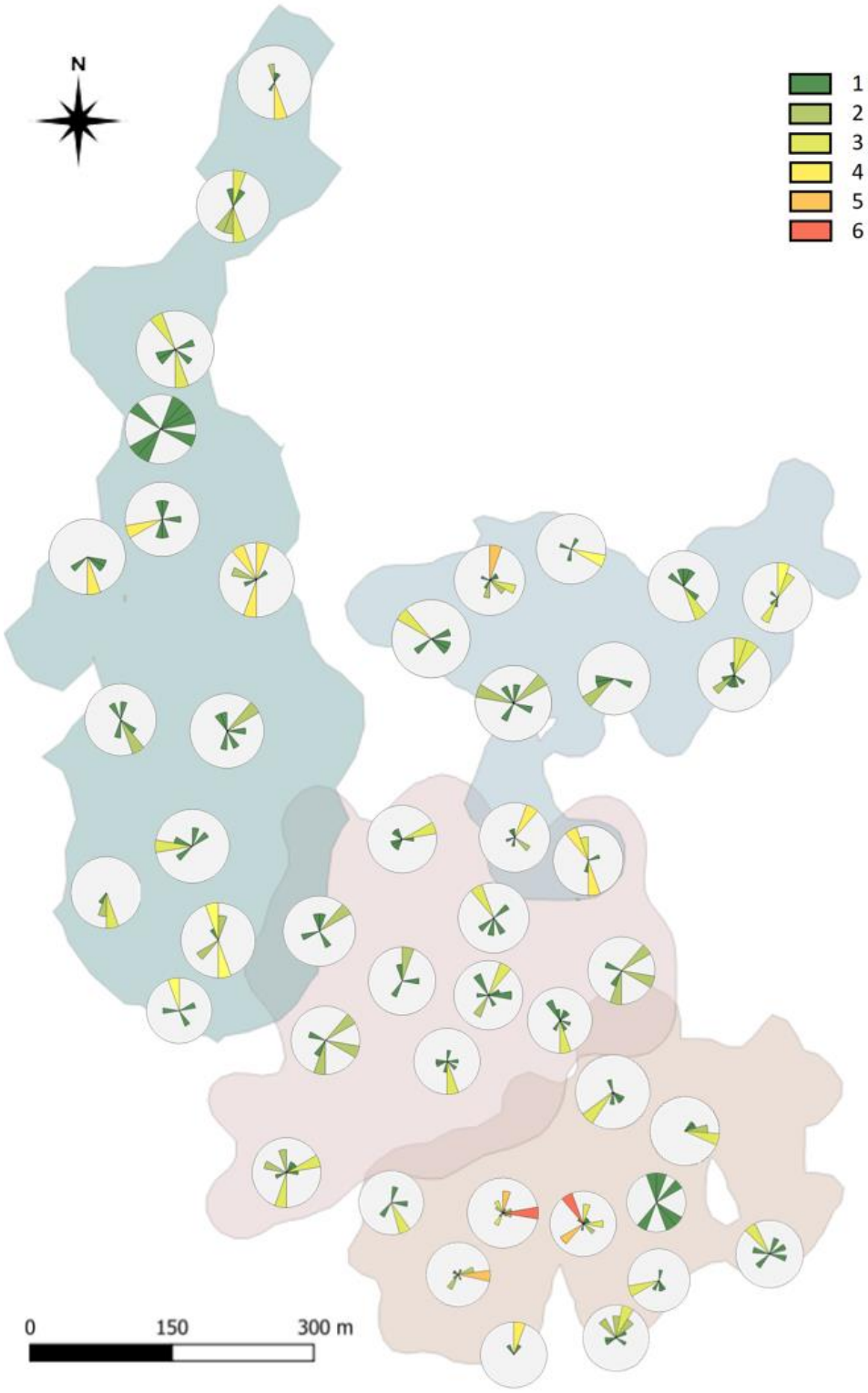


Figure 3.8b Subset of all described arrival and departure angles combined to reach revisited feeding sites in observed black howler movement. The legend illustrates the total number of times that each direction was reused to reach these revisited feeding sites.

I detected a total of 81 nodes across all simulated route networks and 112 across observed route networks (Fig. 3.9; Table 3.6). Similarly, the number of edges was higher in the observed route networks than in the simulated ones but the number of connections per node (degree) remained similar. Simulated and observed networks showed similarities in their density and clustering parameters. Networks constructed from real observations showed an overall higher diameter than simulated networks but this effect was mainly driven by one of the groups (Naha) whose diameter was twice the size it respective simulated network. I found statistical differences at node level, where real route networks showed higher levels of strength than simulated networks ($mean_{simulated}$ = 6.5 ± SD 2.9; $mean_{real}$ = 9.7 ± SD 4.6). In addition, simulated route networks showed longer average shortest paths ($mean_{simulated}$ = 260.8 ± SD 187.0 m) and higher degrees of closeness ($mean_{simulated}$ = 0.005 ± SD 0.001) than real route networks ($mean_{real}$ = 230.8 ± SD 156.8 m; $mean_{real}$ = 0.003 ± SD 0.001; Fig. 3.10).

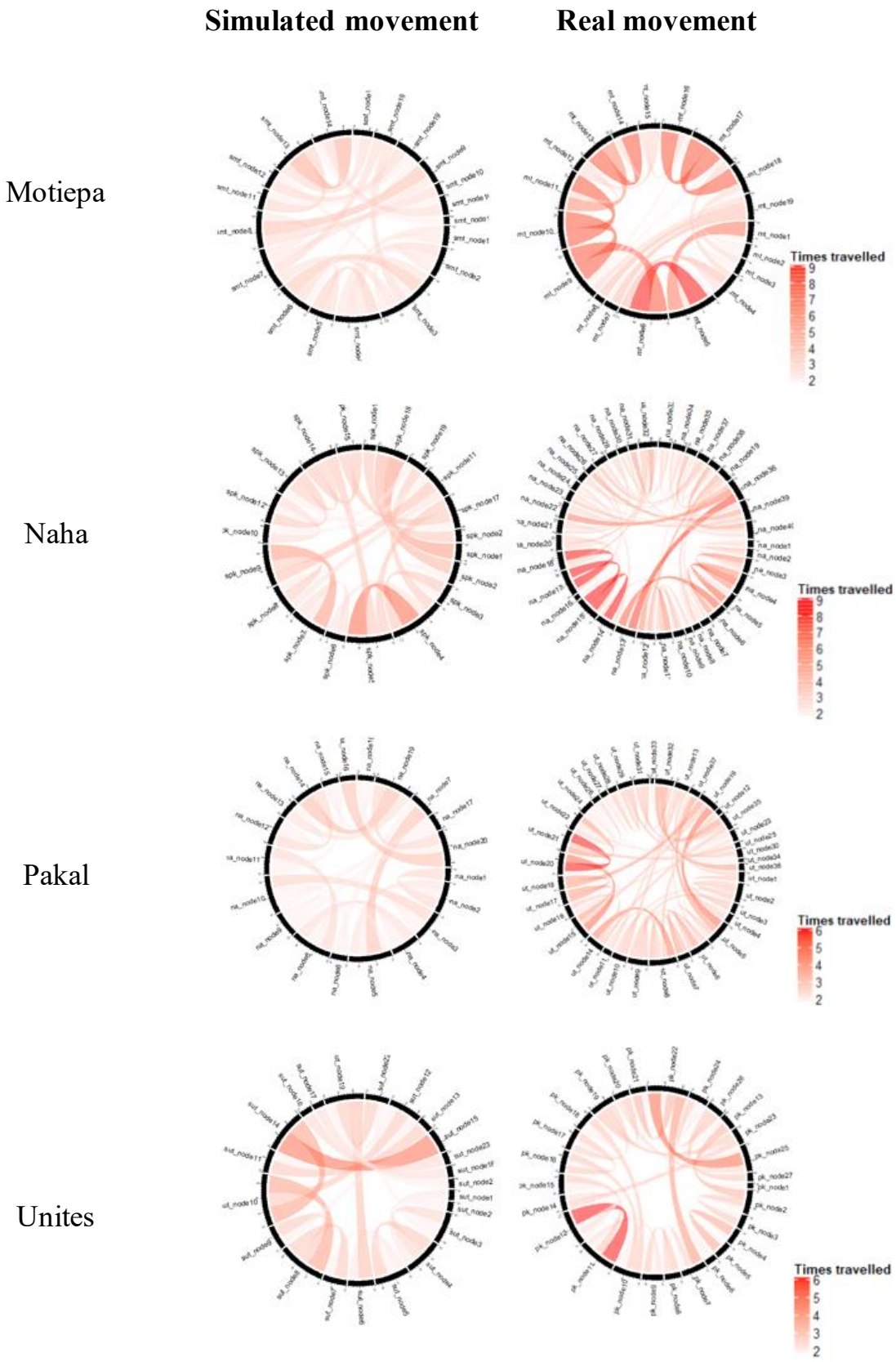


Figure 3. 9 Chord diagrams describing the number of connections among nodes for each study group and simulated data. The code used for each node is shown in the outline of each plot and the frequency of travel across each route segment connecting nodes is described in a coloured gradient (*red*: real movement; *grey*: simulated movement).

Table 3. 6 Summary of the statistical analyses comparing the properties of real and simulated route networks at global level.

Group	N nodes	N edges	Degree	Density	Network diameter	Clustering
Simulated movement						
Motiepa	19	25	2.63	0.15	25.85	0.23
Naha	20	24	2.40	0.14	20.37	0.12
Pakal	20	26	2.60	0.13	23.43	0.15
Unites	22	21	1.90	0.09	25.67	-
Average	**20.25**	**24**	**2.38**	**0.12**	**23.83**	**0.17**
Real movement						
Motiepa	19	27	2.84	0.16	27.11	0.15
Naha	29	35	3.13	0.08	47.47	0.21
Pakal	27	61	2.59	0.10	26.85	0.14
Unites	37	49	2.65	0.08	27.07	0.08
Average	**28**	**43**	**2.81**	**0.11**	**32.13**	**0.14**

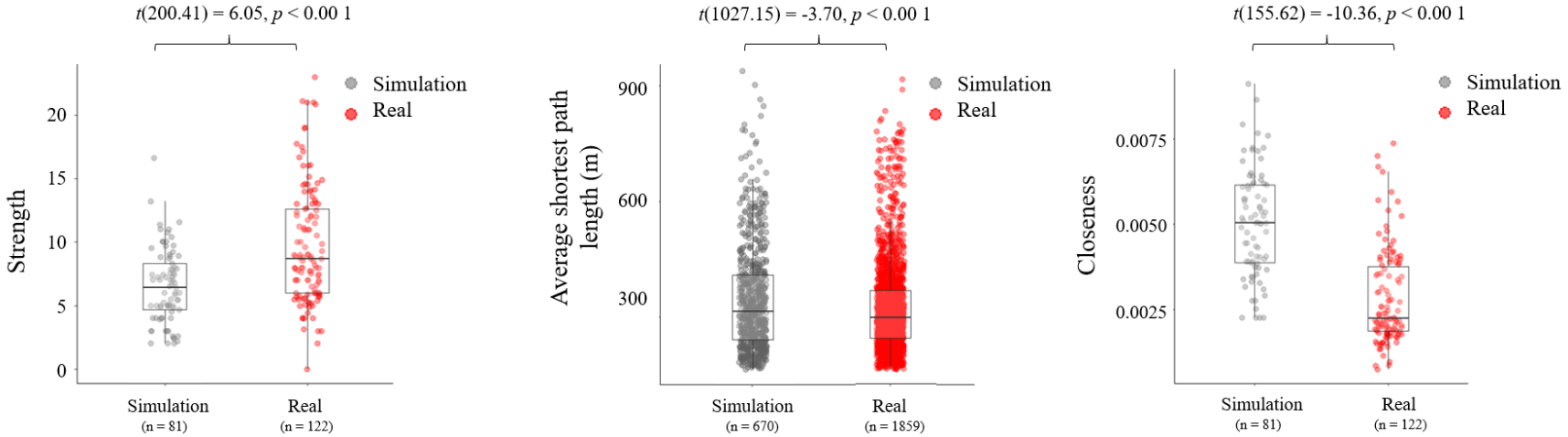


Figure 3. 10 Summary of the statistical analyses comparing the properties of real and simulated route networks at local level

3.4 Discussion

I evaluated the cognitive maps used to navigate by black howlers comparing observed movement patterns with computer-generated random movement, which acted as a control. Black howlers repeatedly navigated through habitual route segments within the home range of the study groups, as did the simulated agents. However, black howlers approached and departed from revisited feeding sites using a small subset of directions while simulated random agents used almost twice as many directions as howlers. In addition, nodes were also present in the route network described by simulated agents but in a smaller number and connected in a less efficient manner than observed route networks. These results suggest the importance of in-depth analyses when comparing simulated versus observed movement patterns and validate using random movement as control. The most parsimonious explanation of the movement characteristics reported in this chapter is that black howlers use a route based cognitive map as their main navigation strategy.

In both sets of movement patterns, there was a high tendency to navigate more frequently within than outside habitual routes. Even though the accumulated number of metres travelled within route networks did not differ among simulated and observed movement patterns, the frequency of use of habitual route segments was significantly higher in observed movement patterns. Black howlers showed a clear asymmetry in the frequency of use of route segments, travelling through the same sequence of trees even in nine non-consecutive weeks. Contrary to the observed data, simulated agents never travelled through the same segment in more than four different occasions. The high frequency of use of habitual route segments in specific locations might respond to potential local advantages such as reduced energetic expenditure or availability of food

resources. Such potential advantages are explored in the next chapter. Interestingly, this study differs from previous evidence in the fact that there is no clear difference among overlap degree in core versus non-core areas (tamarins, Garber & Porter 2013; Porter & Garber, 2014; black capuchins, Presotto & Izar, 2010; African elephants, Presotto et al., 2019). Likely, black howlers gathered enough spatiotemporal knowledge to expand their route network through their entire home range. By establishing a set of routes all over their home range, access to further away food resources can occur within few decision steps. In addition, relying on core area delineation as indicative of familiarity may not be the best proxy for black howlers at PNP. The relatively high daily path length in relation to the reduced home range size of black howlers at PNP suggests that black howlers constantly navigate throughout their entire range every few weeks. Therefore, the entire home range could likely be considered as a familiar area for black howlers. Evaluating the ranging patterns of howler populations inhabiting large home ranges would truly indicate whether howler monkeys are able to engage in flexible movement patterns in unfamiliar terrain or still rely on routes (Fortes et al., 2015; Presotto et al., 2019).

The unexpected high degree of overlap among paths of simulated agents can be interpreted as a reliable representation of black howlers' movement patterns, which successfully mimicked real movement patterns (Garber & Hannon, 1993). An alternative explanation would be that the selected thresholds in the protocol to determine inter-path overlap was not conservative enough (Bebko, 2018; Porter, 2020). I used the criteria described in the literature to facilitate future comparisons among species but black howlers scale of movement may require a species-specific approach. While using GPS accuracy seems highly reliable to determine the radius of the

buffering areas, selecting too small values as minimum segment length can lead to an overestimation on the use of routes to navigate. On the other hand, I did not incorporate landscape restrictions within the simulations (i.e., increased slopes, canopy gaps). Incorporating PNP's landscape heterogeneity into the movement choices of simulated agents instead of letting them wander around the entire home ranges freely will likely further increase path overlap (Suarez et al., 2014). After having settled the ground with the present research, I suggest a modified version of the model in which movement will be constrained by the real route network, which was likely shaped according to the natural limitations of the landscape at PNP. Examining the frequency of use of different route segments by simulated agents and black howlers will indicate the importance of spatiotemporal knowledge of food resources and the energetic costs of travelling throughout the route networks (Suarez et al., 2014).

Black howler at PNP systematically moved towards and away from revisited feeding sites through the same set of directions and, therefore, the same routes. Contrary to this, simulated agents kept accumulating different arrival and departure directions with the course of time (as in Garber & Hannon, 1993). This finding are in line with the high degree of inter-path overlap and suggests the use of a route based cognitive map both in large- and small-scale scenarios (Urbani, 2009). Yet, arboreality may impose spatial constraints triggered by the forests structure such us inter-tree degree of connectivity (Hopkins, 2011; McLean et al., 2015). Even though PNP has been preserved for nearly four decades (Figueroa & Sánchez-Cordero, 2008), two of the study groups overlapped their home ranges with pasturelands and there were occasional physical obstacles (i.e., water flow, Mayan ruins) that limited the presence of vegetation (Van Belle & Estrada, 2019). Therefore, access to specific trees may be limited to a

small subset of directions in some cases. However, the fact that all observed groups of black howlers reached a plateau in the number of different routes used to travel through revisited feeding sites reflects a high degree of consistency among these results across different environmental conditions. De Raad & Hill, (2019) argued that using linear statistics for directional data can produce different outcomes than circular statistics specifically designed for directional data. However, the most common circular tests lack statistical power even after doubling sample sizes (Ruxton, 2017; Landler et al., 2018). In addition, circular tests typically evaluate whether the distribution of directions around a given centre is clustered or uniform without specifying the number of clustered locations (Ruxton, 2017). Since my findings corroborate the results reported in baboons by De Raad & Hill (2019), the method I used to estimate differences in arrival and departures appears valid and consistent with previous evidence.

I found relevant evidence regarding the structure and efficiency of route networks in black howlers by applying methods developed in the field of graph theory. To date, this is the first time that spatial network analyses have been applied to multiple groups of wild primate's route networks, which sums up the scarce previous literature in other animal taxa (pigs, *Sus scrofa*, Nöremark et al., 2011; sharks, *Syliorhinus canicula* and *Carcharhinus perezi*, Jacoby et al., 2012). Differences in strength among real and simulated networks highlighted that howlers navigated more often through some connections than others while simulated agents were relative homogeneous in their movement options. Asymmetrical differences in the frequency of use of connections are typically found in networks as the worldwide air-transportation network (ATN), mainly due to the imposition to passengers to travel through specific airports (Barthélemy, 2011). In addition, ATN is characterized by a strong correlation between number of

connections per node (degree) with its strength values (Barrat et al., 2005), which was also found in black howlers' route networks (Fig. 3.11). Such correlation has been argued to reveal the importance of topography in the formation of networks since the more spatially constrained a node is, the lower the number of connections to other nodes will be and the more asymmetrical their travelling frequency will be throughout the network (Barrat et al., 2005; Barthélemy, 2011).

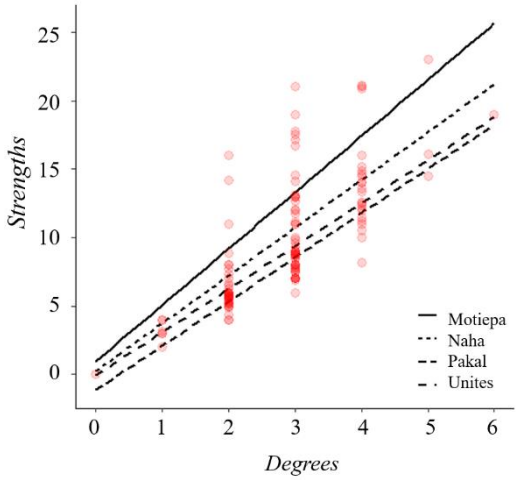


Figure 3.11 Weighted strengths versus degree of connectivity for black howlers' route networks (spearman rank correlation test: r_s = 0.85, p-value < 0.001).

The average shortest path to travel among nodes was shorter within black howlers' route networks than within simulated route networks even though the overall diameters of black howlers' networks were larger than simulated networks. Thus, while the shortest path to reach any node within the network encompassed 4.1 ± 2.1 nodes along an average of 230.8 m for black howlers, simulated agents needed to go through 3.7 ± 1.9 nodes along 260.8 m on average. This evidence suggest that black howlers' route networks were structured to cover a large proportion of their home ranges while

promoting efficient navigation among distant areas (Soh et al., 2010). In addition, the low degree of centrality in real route networks suggested that black howlers did not depend on few, specific trees to bridge areas within their home range. Due to structural dynamisms of rainforests characterized by trees constantly falling (Martinez-Ramos et al., 1998), non-centralized route networks in arboreal tropical species would be highly advantageous to avoid losing access to specific areas and ease the process of finding alternative routes (Jacoby & Freeman, 2016). Altogether, black howlers composed and structured their route networks more efficiently than simulated agents. Since the goal of this chapter was to describe evidence supporting the use of cognitive maps rather than developing new analytical tools, I focused on descriptive results and superficial statistical analyses. Yet, there is potential to apply advanced network models in the present dataset that will enhance the overall picture depicted here. While network analyses in animal movement have been used as powerful tools to examine disease transmission and social dynamics in wild populations (Barthélemy, 2011; Nöremark, 2011), there is increasing potential for its application into the study of spatial cognition that will be likely developed within the next years (Jacoby et al., 2016).

Overall, the combination of evidence highlights that black howlers strongly rely on route networks to navigate, which implies memorising a series of landmarks associated with habitual routes instead of using an Euclidean navigation system. My results are consistent with evidence from other field sites in mantled howlers and brown howlers (Milton 1981; Hopkins 2011; 2013; Pereira, 2008; but see Garber & Jelinek, 2006). I did not find evidence suggesting a combination of both cognitive strategies as shown in other primate species (Valero & Byrne, 2007; Presotto & Izar 2010; Garber & Porter 2014; Schreier & Grove, 2014; Presotto et al. 2018). Yet, addressing multiple

evidence associated with cognitive maps navigation strategies was necessary to frame black howlers' spatial skills accurately (De Raad & Hill, 2019). After establishing a foundation for the navigation strategy used by black howlers, the next step is to elucidate the potential benefits associated with a navigation strategy that by definition constrains movement. Likely, route navigation might be an option rather than a cognitive imposition, which can enhance animal's movement by minimizing the costs of travelling (Bertolani, 2013).

Chapter 4: Arboreal navigation and route selection: energetic implications associated with tree monitoring and landscape attributes

4.1 Introduction

Animal movement involves a constant trade-off between information processing and energy balance that has led to the evolution of different navigation strategies (Couzin, 2009). Although following routes might constrain an animal's movement flexibility, it may nonetheless enhance its overall energy balance (Di Fiore & Suarez, 2007). The accumulation through generations of environmental information within a group of animals can minimise the cost of travelling by optimising the selection of routes to navigate (Spiegel & Crofoot, 2016). For instance, pigeons (*Columba livia*) that travelled in pairs increased the linearity of their homing route over the course of multiple generations (Sasaki & Biro, 2017). Similarly, translocated bighorn sheep (*Ovis canadiensis*) adjusted the location of their migratory routes through time in order to avoid energetically costly areas of the landscape (Jesmer et al., 2018). Thus, combining individual experiences with information sharing leads to economising travelling costs by selecting routes based on the abundance and distribution of food resources (Denny et al., 2018), the resistance of the landscape (e.g., mountain ridges; Howard et al., 2015) and avoidance of predators or conspecifics (Avgar et al., 2015).

A major potential advantage associated with the habitual use of route segments is the ability to regularly monitor the phenological states of food trees that are located within the visual range of animals while travelling (Milton, 1981; Janmaat et al., 2013). By travelling through areas with a high number of potential food resources, animals may benefit both cognitively and energetically (Fagan et al., 2013). The cognitive load

stored and constantly updated should decrease considerably when only needing to associate multiple food trees with particular travel routes (Buzsáki & Moser, 2013). Instead, memorising the location and phenological stages of multiple single food trees scales up exponentially the cognitive demands of navigation (Dicke & Roth, 2016). Reducing the cognitive load may decrease the amount of energy allocated to brain tissue, which in turn can be employed for other physiological processes and/or behavioural activities (Isler & van Schaik, 2006). Additionally, by clustering the food resources along routes, animals would reduce their need for exploratory behaviour and decrease the energy spent on travelling (Milton, 1981).

Similarly, the structure of the space or landscape that is traversed by an animal or a group is undoubtedly linked to the energetic cost of locomotion (Shepard et al., 2013; Halsey, 2016). Different features of the landscape, such as slope, elevation or substrate, determine the energetic cost of locomotion through an area, which in turn will influence the selection of frequently used routes (Halsey, 2016). In terrains with steep slopes, terrestrial animals need to increase their kinetic energy as they move up a slope, increasing the biomechanical and metabolic cost of moving (Shepard et al., 2013; Wall et al., 2006). For instance, Newmark & Rickart (2012) showed that wild ungulates (*Odocoileus hemionus* and *Cervus elaphus*) repeatedly used routes that avoided steep slopes to economise energetic expenditure. Similarly, slope may increase travelling costs in arboreal animals if they remain at a relatively constant height in trees (Thorpe et al., 2007). Contrarily to the energetic benefits of avoiding slopes, detectability of further away food resources and neighbouring conspecific groups while travelling may increase in areas with pronounced slopes (Gregory et al., 2014). Movement decision-making processes would incorporate such information obtained along the way, which may

enhance both terrestrial and arboreal animals' foraging efficiency and home range defensibility (Fagan et al., 2013; Spiegel & Crofoot, 2016).

In addition, the characteristics of the substrate (i.e., medium over or on which an animal moves) will determine the energy expenditure of an animal (Crête & Larivière, 2003; Shepard et al., 2013). In the case of arboreal animals, the characteristics of the substrate, specifically level of inter-tree connectivity, not only influence movement costs but also the availability of substrates themselves (i.e., presence of canopy gaps in the forest or deforested areas; Gouveia et al., 2014). Dense canopies have been shown to influence positively the selection of routes in multiple arboreal animals (ringtail possums, *Hemibelideus lemuroides*, Wilson et al., 2007; Lumhotz's tree kangaroo, *Dendrolagus lumholtzi*, Heise-Pavlov et al., 2011; mantled howler monkeys, *Alouatta palliata*, Hopkins, 2011; orang-utans, *Pongo pygmaeus*, Davies et al., 2017).

Here, I explore different factors that influence the route selection process of an "energy minimiser" (Dias & Rangel-Negrín, 2015) – a group living arboreal primate in a variable terrain, the black howler monkey. Howlers have evolved an enlarged digestive system, which together with their high gut microbiome adaptability allow them to increase the consumption of leaves even above 90% (Milton, 1984; Amato & Righini, 2015; Dias & Rangel-Negrín 2015). The lack of a specialised stomach and foregut fermentation that is present in colobines induced howlers to rely on hindgut fermentation that occurs after the small intestine (Amato & Righini, 2015). As a consequence, the slow transit and long retention rates in the digestive system associated with howlers' leaf-based diet reduces the availability of metabolic energy (Milton, 1981). Hence, howlers have been described to adjust their activity budget and daily path

length in periods of food scarcity to maximise their energetic balance and counteract the effect of their digestion (Agostini et al. 2010).

In addition, black howlers engage in highly selective foraging patterns to fulfil their nutritional demands using many different individual trees to forage within and between years (Amato & Righini, 2015). Memorising all these locations and their respective phenological cycles is assumed to be challenging given the relatively small brain size of these primates (Milton, 1981). By locating travelling routes near potential food resources, black howlers may benefit from reducing their cognitive load by continuously monitoring the status of food resources while travelling (Hopkins, 2011). Further, the study was conducted in a variable terrain where topographic attributes could influence the costs of movement from changes in elevation to occasional gaps of forest coverage (Barnhart, 2001; Estrada et al., 2002). Hence, the selection of routes to navigate will reflect the energy minimising strategy of black howlers by avoiding such costly attributes of the landscape.

First, I hypothesised that black howlers would select their routes to monitor food resources. I predicted that routes would intercept more food resources than by chance and that the number of food resources intercepted per metre travelled would increase with route's usage frequency. Second, I hypothesised that routes were selected to avoid costly features of the landscape. I predicted that terrain slope and canopy gaps would negatively influence the occurrence of routes while elevation would positively influence the occurrence of routes only when food resource visibility decreased.

4.2 Materials and Methods

4.2.1 Data Collection

See section 2.1 – 2.4.

4.2.2 Data analyses

The methods used to construct black howlers' route networks are described in section 3.2.3. I determined the influence of feeding tree (FT) distribution on the location of route networks by randomly simulating the same number of locations as recorded FT within the home ranges of each study group excluding areas with no forest coverage (Suarez, 2014). Each simulation was run with the R package *rgdal* 1.3-6 (Bivand et al., 2018) and was repeated 10,000 times. Finally, I traced a series of buffers with 5 m increment from 5 m to 20 m around routes of each study group, and recorded the total number of FTs and simulated locations that fell within each buffer to statistically compare it (see below; Presotto & Izar, 2010). Since I performed 10,000 simulations, I calculated the mean number of locations that fell within each buffer for each study group to compare it with the number of observed FTs.

Subsequently, I tested whether the number of FTs visually intercepted along route segments increased with the frequency these routes were reused. For this, I calculated the number of FTs intercepted per metre travelled along each segment to account for segment length. I determined the topographic attributes of the landscape using an archaeological map of the Mayan city of Palenque (Barnhart, 2001). I georeferenced this topographic map and triangulated the three-dimensional locations into ArcMap 10.4 to create a Digital Elevation Model (DEM). I overlaid a grid layer of 10x10 m quadrats and extracted values for slope and elevation for each quadrat using

the Spatial Analysist tool from ArcMap 10.4. See Fig. 4.1 for a visual representation of the route networks used by the study groups overlaid on top of the DEM.

I calculated slope as the difference between the highest and lowest point within each quadrat and elevation as the elevation of the absolute centre of the quadrat. I marked the edges of canopy gaps in the field using a GPS device and corrected them using satellite imagery. I created a buffer of 25 m from the centre of each quadrat and calculated the percentage overlap between such a buffer and the recorded canopy gaps.

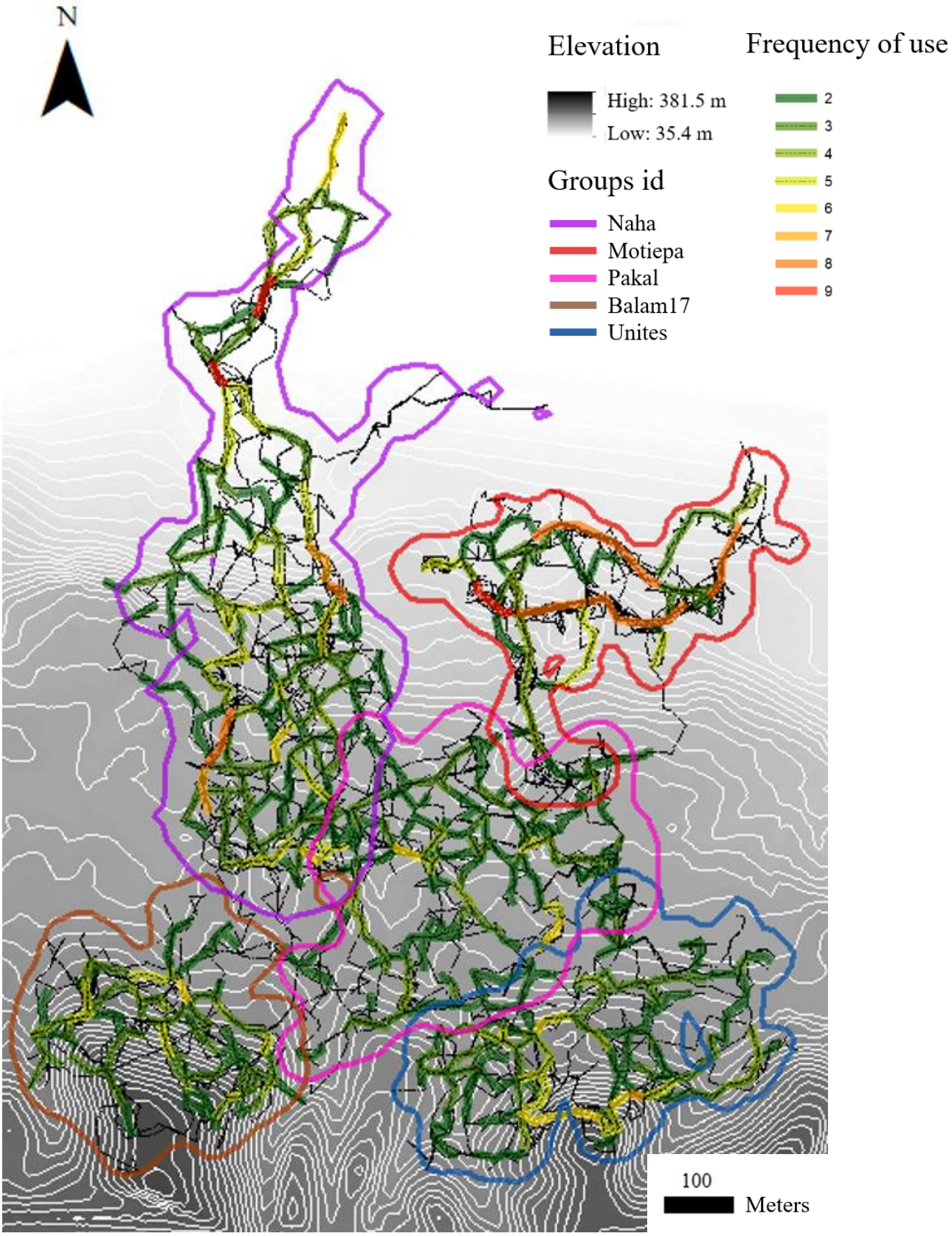


Figure 4. 1 Three-dimensional representation of PNP with its natural elevations (dark green), howler monkeys home ranges, all marked food trees (black points), and route networks of the studied population based on data from September 2016 until August 2017.

I determined the potential to detect FTs by creating a series of buffers every 5 m from the centre of each quadrat up till 35 m, which is the estimated visual detection distance of howler monkeys (Milton, 1981; Hopkins, 2011). Then, I counted all FTs contained within each buffer including FTs already counted in small buffers embedded in large buffers (e.g., FT counted in 5 m buffers were counted again in 10 m buffers; Fig. 4.2). Subsequently, I calculated the proportion of FTs within the visible range out of all trees of these species within the home range per study group. Per quadrat, values for all buffers were summed and weighted by the number of buffers (N=7). By including previously counted trees in smaller buffers into large buffers in this visibility index, I emphasised the importance of FTs near the centre of the cell that were more probable to be monitored than FTs further away.

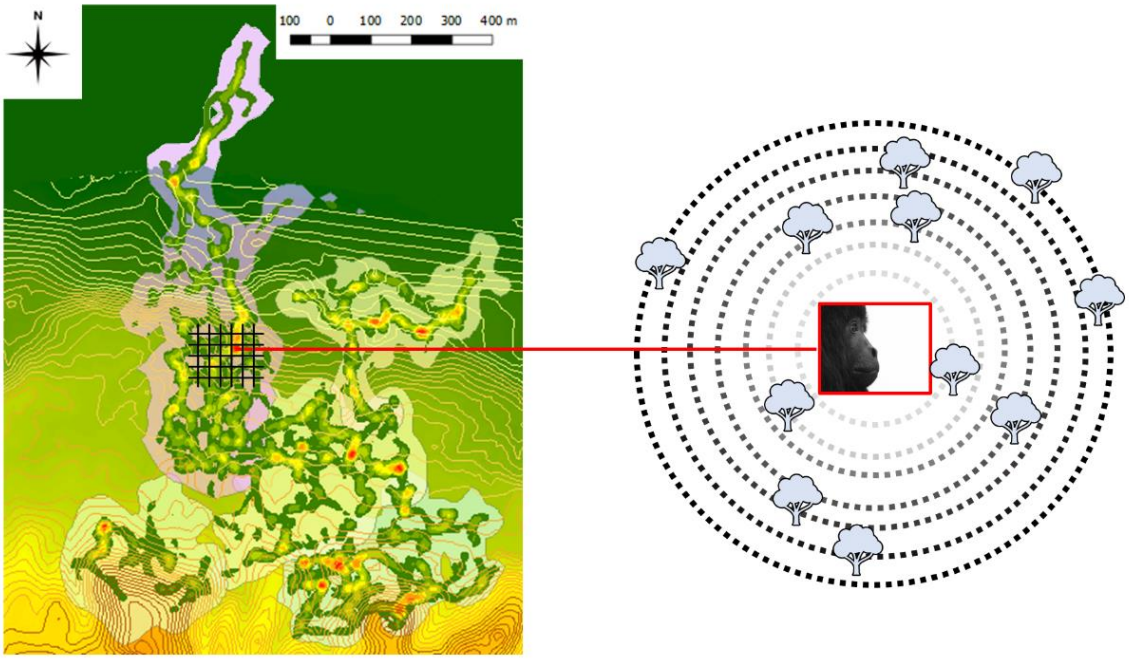


Figure 4. 2 Illustrative example of design procedure to estimate visibility throughout the study area in which black howlers' home ranges are overlaid on the terrain's elevation. The frequency of use of the route network is illustrated from dark green (low) to red (high).

4.2.3 Statistical analyses

I fitted two LMMs to determine the monitoring behaviour of black howlers. First, I tested whether routes intercepted more FTs than by chance by using the number of locations intercepted per buffer around the route network as response variable and type of location (real or mean of simulated FT) as predictor variable. For the second model, the response variable was the number of FTs intercepted per metre travelled and the frequency of use of a certain route segment was the predictor variable. For both models, buffer size was used as control variable since larger buffers would likely intercept a larger number of FTs than small buffers. I excluded one study group (Balam) from these two models because its composition and home range location changed in January 2017 (Van Belle & Estrada, 2020).

In addition, I fitted two GLMMs with a binomial error structure and a logit link function to test the influence of landscape features on the probability of using a quadrat to locate a route within a route network. For these models, the response variable was presence/absence of routes for each quadrat, either used at least twice or at least four times, respectively. For both models, the predictor variables were elevation, slope (square-root transformed), percentage of area covered by gaps, and the visibility index of FTs per quadrat. I included an interaction between elevation and visibility in both GLMMs since we predicted that black howlers located routes to navigate in elevated areas within their home range only when visibility to food resources decreased.

To account for potential differences among groups, I included group ID (N=5) as a random variable (random intercept) in all models. In order to allow for fixed effect predictors to vary among the levels of the random effect variables, random slope terms were included in the models. In addition, I incorporated two control variables:

intergroup overlap (whether a certain quadrat was used by multiple groups or not) and home range location (whether the quadrat fell inside or outside the group's core area).

I controlled for spatial autocorrelation by determining an autocorrelation term from the full model and subsequently including this term as a control variable in a newly fitted full model (Janmaat et al., 2016). These terms were calculated as the average of the residuals from the original model (for all data points from the same group) weighted by the distance to the particular data point. The weight followed a normal distribution for which the standard deviation (*D*) was optimised such that the log-likelihood of the full model including the autocorrelation term was maximised (here: *D* = 5-7; based on Fürtbauer et al., 2011).

4.3 Results

We recorded a total of 1528 travel bouts (mean: 305.6 ± SD 43.9 travel bouts per group). On average, the length of an individual travel bout was 65.3 ± SD 57.5 m and the daily path length was 365.8 ± SD 199.2 m, ranging from 28.2 m to 1022.8 m. Between 64.5% and 75.1% of the travel bouts fell within a route network (route at least used twice), which had a mean length of 3.2 ± SD 1.2 km per group. Home range size ranged between 7.1 – 15.3 ha while the relative difference in elevation within each study group was 86.2 ± SD 24.8 m amongst quadrats (Table 4.1).

Table 4. 1 Demographic and environmental summary of the study groups and areas: number of individuals present in each group during the study period; estimated home range size using Kernel 95% estimator; mean number of feeding trees (N FT) visually detected from the route network till 20 m distance; elevation and slope range within each study group; and, area covered by canopy gaps in hectares and percentages for each study group.

Group ID	Group size	HR size (ha)	N FT visually detected (mean ± SD)	Elevation range (m) (min - max)	Slope range (°) (min - max)	Gaps (ha) (% coverage)
Balam	3 - 4	10.3	-	170.5 – 260.0	0.6 – 39.4	0.3 (3%)
Motiepa	6 – 8	7.1	161.8 ± 36.9	96.4 – 173.8	0.3 – 29.4	0.9 (12.9%)
Naha	5 - 8	15.3	173.8 ± 35.5	65.0 – 190.4	0.2 – 45.2	1.8 (11.9%)
Pakal	7 - 9	10.6	186.3 ± 38.8	152.6 – 212.8	0.6 – 29.4	0.3 (3%)
Unites	4	8.6	102.8 ± 22.5	178.1 – 264.9	1.5 – 40.9	0.3 (3.3%)

4.3.1 Monitoring of FTs

The total number of FTs potentially visible from the route network (mean 156.12 ± SD 44.05 trees per group, Table 4.1) was significantly higher than would be expected by chance (mean 121.96 ± SD 46.42 locations) as shown by the likelihood ratio test (χ^2 = 7.9, Estimate = -34.2 ± 6.9, d.f. = 1, *p*-value = 0.005). Similarly, the number of FTs visible from the route network per metre travelled increased with increasing frequency of use of the segment (likelihood ratio test: χ^2 = 15.12, Estimate = 0.35 ± 0.04, d.f. = 1, *p*-value < 0.001). For instance, the number of FTs visible along route segments used twice was 0.72 ± 0.43 trees/m while it increased to 1.12 ± 0.52 trees/m in segments used four times and to 2.46 ± 1.97 in segments used seven times (Fig. 4.3).

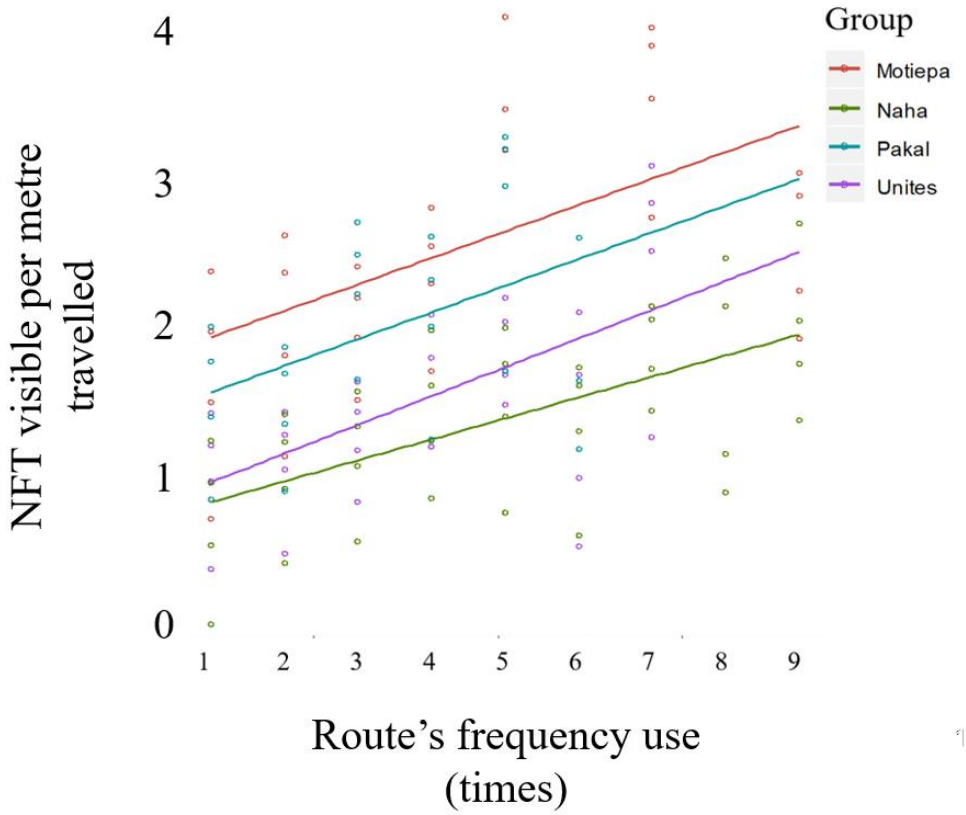


Figure 4. 3 Fitted linear regression of number of feeding trees (FT) intercepted per metre travelled against frequency of use of route's segments. The plot shows the four study groups that were included in this analysis. Note that route segments used once were travel bouts that never overlapped other travel bouts.

4.3.2 Landscape attributes

The likelihood-ratio tests indicated that the GLMMs for routes used at least twice and routes used at least four times were significant (Table 4.2). The probability of a quadrat containing a route that was used at least twice increased with visibility of FT but decreased with presence of canopy gaps. After removing a non-significant interaction from the full model, I did not find a significant influence of either elevation or slope on the probability of a quadrat containing a route used at least twice.

Similar to the previous model, routes used at least four times were significantly influenced by the visibility of FT. Contrarily, there was not a significant influence of gap presence on locating a route used at least four times. There was a significant effect of the interaction between elevation and visibility of FT in the model (Fig. 4.4). Even though the effect of slope in the model was not significant, there was a positive trend towards selecting routes used at least four times in quadrats with highly pronounced slopes.

Table 4. 2 Results of two GLMMs testing the influence of different landscape attributes on the probability occurrence of a route segment used at least twice and four times within a certain quadrat.

Response variable	Probability of locating a route used at least twice			Probability of locating a route used at least four times		
Full null model comparison	$\chi2 = 23.2$, d.f. = 5, p-value < 0.001			$\chi2 = 18.8$, d.f. = 5, p-value = 0.002		
Predictor variable	**Est.**	**s.e.**	***p*-value**	**Est.**	**s.e.**	***p*-value**
(Intercept)	-0.156	0.574	[a]	-3.126	0.298	[a]
Slope	0.139	0.104	0.182	0.390	0.139	0.058
Presence of canopy gaps	-0.803	0.115	**0.001**	-0.354	0.186	0.128
Elevation	0.446	0.328	0.198	0.944	0.550	0.173
Visibility of FT	0.896	0.213	**0.006**	0.967	0.246	**0.010**
Elevation * Visibility of FT	-0.280	0.210	0.273	-0.439	0.140	**0.041**
Overlapping area [b]	0.274	0.136	0.054	-1.000	0.203	**0.003**
Location within the HR [b]	-0.538	0.442	0.255	-0.724	0.499	0.190
Autocorrelation term [b]	2.487	0.072	**< 0.000**	2.943	0.100	**< 0.000**

[a] Not shown because of having no meaningful or very limited interpretation.

[b] Represent control predictors included in the model

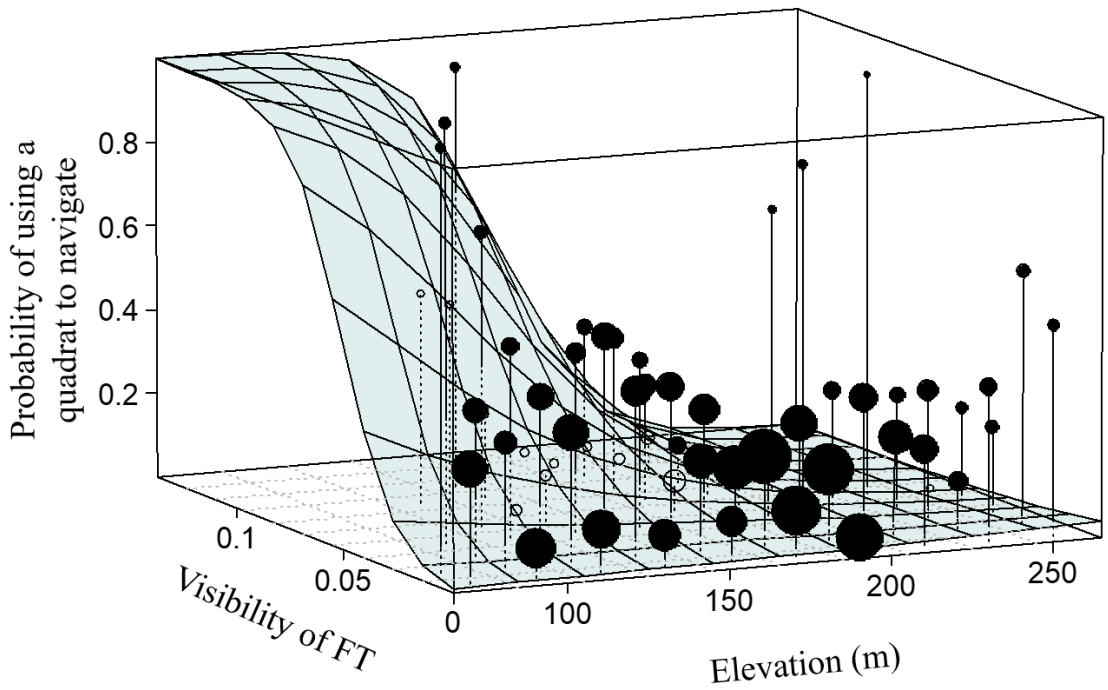


Figure 4. 4 Probability that black howler monkeys selected a quadrat to navigate at least in four different occasions in relation to the relative elevation within their home range and the visibility of FT. The height of spheres represents the probability that a certain quadrat was chosen to navigate per combination of elevation and visibility of FT. Each surface (i.e. square) represents the expected probability of a quadrat to be chosen according to the model (conditional on all other predictors being set at their average value). Sphere size corresponds to the relative number of observations, with closed circles being above the model surface and open circles below.

4.4 Discussion

These findings show that black howlers navigate along a route network where their occurrence is linked to the distribution of potential food resources and the attributes of the landscape. Even though following specific routes to navigate can limit an animal's movement options (Poucet, 1993), black howlers seem to counteract such constraints by optimising the location of their habitual routes. The accumulation of knowledge over generations may have led to the selection of routes that minimises energy expenditure and favours tree monitoring while travelling (Spiegel & Crofoot, 2016; Berdahl et al., 2018).

Black howlers at PNP visually intercepted a higher number of food resources while travelling along their route networks than they would by chance. If black howlers would have had Euclidean cognitive abilities, they would have avoided traveling in between food resources in a repeated, sequential manner. Instead, they chose a better-than-chance strategy by travelling repeatedly through the same sequences of trees that supported resource monitoring on the move (Milton, 1981; Hopkins, 2011). Also, the number of food resources intercepted increased with the number of times that a certain route segment was used. Hence, frequency of use increases the appearance of a regular monitoring route. By securing foraging success while reducing the number of locations that need to be memorised, the complexity of processing movement decisions decreases (Janson, 2019). In addition, a reduction in the number of operative elements to include in the cognitive processes will enhance the planning abilities of cognitively constrained animals (Fagan, 2013). Indeed, arboreal animals are able to plan future movements using the information obtained from monitoring feeding trees (Janmaat et al., 2012). Various animal species have been shown to re-direct their movements towards locations or trees of a certain species after having detected available food within other similar

locations (Hopcraft et al., 2005; Raby et al., 2007; Ban et al., 2016). By gathering ecological information on patterns of food availability, animals increase the predictability of a successful foraging event across heterogeneous landscapes (Janson, 2019).

The importance of visual access to potential food resources was consistent in our results. Apart from locating routes within the visual detection distance of food resources, elevated areas were selected to navigate when food resources were not visible. Hence, black howlers navigated through elevated areas to increase the visual overview of the landscape and detect food resources over long distances. Arboreal animals in rainforests need to find mechanisms to enhance their visual window typically obstructed by foliage, tree trunks or lianas (Janson & Bitetti, 1997). Thus, the selection of ridgetops and large trees to navigate is a common behaviour found among arboreal animals (Garber & Jelinek, 2005; Di Fiore & Suarez, 2007; Gregory et al., 2014). Exposure to aerial predators increases when travelling frequently through more elevated areas (Boinski et al., 2000). In fact, I found that such interaction between elevation and visibility of food resources was only present on route segments used on four different occasions or more. Travelling through such segments will not only increase black howler's exposure to predators but also the predictability of being found by predators. Therefore, arboreal animals are likely to develop strategies to avoid predators in their travelling patterns, such as engaging in brief pauses during travelling bouts to scan the surroundings or avoid using the same route within the same week (Garber & Bicca-Marques, 2002). Additional strategies such as predator-prey temporal niche partitioning, group's shared travelling vigilance or collective shared decision making should be addressed to understand the socioecological evolution of arboreal species.

Even though I predicted that black howlers at PNP would avoid slopes to economise the expenditure of energy, I found a positive trend on the selection of routes associated with increased slope. The energetic cost of travelling along slopes for a large bodied animal represents a major challenge at ground level (Halsey & White, 2017) but it may not be the case once in the trees. Contrary, travelling through sharp slopes may increase visual access over the landscape as discussed above (Gregory, 2014). Hence, patterns found in terrestrial animals cannot be assumed in arboreal animals since arboreality may impose other energetic challenges (Halsey, 2016). Since howler monkeys' main locomotor strategy is quadrupedalism (Youlatos et al., 2015), moving vertically – descending to the ground and re-ascending to the canopy – increases the number and complexity of movements engaged in by howler monkeys (McLean et al., 2016). Thus, selecting areas with a continuous horizontal substrate (or canopy) might be more energetically advantageous than avoiding a terrain's ground slopes (Ancrenaz et al., 2015). Indeed, the models' results show a tendency of selecting areas in which to navigate that avoid proximity to gaps in the canopy, similar to other arboreal animals (Hopkins, 2011; McLean et al., 2016). By avoiding canopy gaps, black howlers improve their overall energetic balance facilitating their locomotion but may also reduce their exposure to pathogens and terrestrial predators (Ancrenaz et al., 2015).

Overall, black howlers' navigation behaviour reflected a process of route optimisation that counteract the effect of different landscape attributes. The selection process incorporated multiple food resources intercepted along routes, which is assumed to reduce their cognitive load by decreasing the amount of information that needs to be stored and processed at each given step. In addition, all the components of "landscapes of energy" (elevation, slopes and substrate) were incorporated in the selection process at different strengths. Thus, I hypothesised that the accumulation of information through

generations within social units, helps small-brained animals overcoming the lack of cognitive power and engage in efficient movement patterns (Spiegel & Crofoot, 2016). Further research should investigate the adaptability of less frequently used routes segments to food availability across years and the influence of additional forest attributes (e.g., crown density, tree architecture, branch resistance, etc.) on the route selection of howler monkeys.

Finally, I would like to remark on the importance of preserving highly used (core) segments within route networks for the conservation of arboreal animals (Gouveia et al., 2014). There is a set of increasingly used route segments that enhance animal's navigation while securing foraging success (Presotto & Izar, 2010). Preserving these sequences of trees through selective logging will be essential for wild populations, especially those facing high rates of habitat loss and deforestation (Estrada et al. 2017).

Chapter 5: Navigation flexibility associated with resource availability, experience and internal motivation

5.1 Introduction

As a rule, adaptive behavioural solutions to predictable ecological or social challenges faced by animals may be favoured by natural selection (Darwin, 1859; Fawcett et al., 2015). Species are characterised by their own distinctive behavioural repertoires, which can also be seen as an intraspecific reduction of behavioural options. The increased robustness of certain behavioural traits can end up challenging a species survival if environmental conditions change either suddenly or too extremely (Snell-Rood, 2013). For instance, Sol et al., (2002) showed that bird species with a higher frequency of foraging innovations tended to succeed more often after being introduced to novel environments than bird species with a lower frequency of innovations. Indeed, behavioural flexibility may be especially beneficial in the current fast-changing world, where habitat change rates and global warming challenge species adaptability at a pace not faced before (Sih et al., 2011; van Schaik, 2013).

The ability of a species to flexibly adapt its ranging patterns to environmental changes may be closely linked to the spatial cognitive skills of the individual (Tucker et al., 2018). In fact, the concept of cognitive maps postulates that individuals with high cognitive skills will perform more flexible ranging patterns (Poucet, 1993). Evidence in the literature highlights the variation in the movement patterns of animals under different ecological and social factors, suggesting that in addition to being socially flexible, some species may also be spatially flexible (Rosati, 2017; Tello-Ramos et al., 2019). A main factor closely related with the use of spatial skills in animals is

environmental heterogeneity (Sol et al., 2008; Fagan et al., 2013). For instance, the distribution of feeding sources conditioned the use of habitual routes by black capuchin monkeys (*Sapajus nigritus*) in south-eastern Brazil (Presotto & Izar, 2010). Capuchins were able to approach high-quality feeding sources from multiple novel routes but under periods of food scarcity the reliance on routes increased (Presotto & Izar, 2010; also Urbani, 2009). White-faced sakis (*Pithecia pithecia*) presented a similar pattern by relying on spatial memory only when preferred fruit sources were available (e.g. *Licania spp*.). In the absence of these sources, sakis became less selective and relied less on memory (Cunningham & Janson, 2013). Cunningham & Janson (2013) argued that rather than the scarcity or abundance of resources *per se*, the uniformity and patchiness of sakis' preferred resource distribution were the crucial factors determining the use of cognitive skills to forage.

The spatio-temporal distribution of preferred feeding sources may drive the navigation strategy employed by primates. According to Fagan et al., (2013), an animal will use the maximum potential of their cognitive capacity to find feeding sources under periods of intermediate preferred food availability. The functionality of their cognitive effort may, therefore, decrease both in periods of high food availability and extreme food scarcity (Fig. 5.1; Fagan et al., 2013). Based on this, we might expect that some animal species may show more flexible spatial skills when navigating throughout scenarios where feeding sources are within an intermediate frame of heterogeneous distribution (Fagan et al., 2013).

The experience of an individual or group within a given area has also been proposed to modify their spatial performance by adjusting their movement patterns while increasing their local knowledge over time (Gale et al., 1990; Spiegel & Crofoot, 2016). Wayfinding abilities in humans in complex urban settings were shown to differ

among adult Italians: individuals with previous experience navigating though complex buildings outperform naïve ones (Iachini et al., 2009). Similarly, Mbendjele children in the Congo basin were found to improve their orientation skills in proximity to their main camp (i.e., within familiar rather than unfamiliar terrain, Jang et al., 2019b). Several nonhuman primate species were shown to follow up this trend by engaging in more efficient movement patterns (i.e., straighter, faster paths) within familiar areas or towards revisited feeding sites (e.g., Weddell's saddleback tamarins, Porter & Garber, 2013; black capuchin monkeys, Presotto, 2009; chimpanzees, Jang et al., 2019a; see

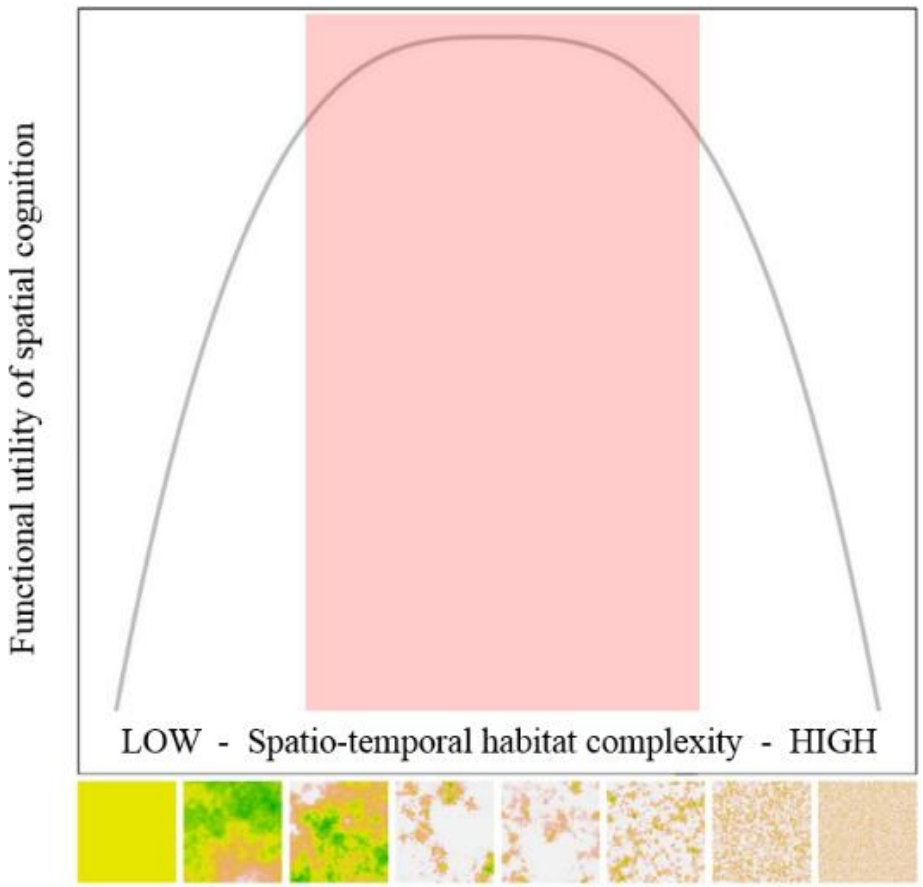


Figure 5. 1 Representation of the functional utility of memory for animal movement in a gradient of spatio-temporal habitat complexity (figure adapted from Fagan et al., 2013).

Trapanese et al., 2019). However, a problem that remains unresolved in the literature is that an area considered as familiar for a specific population might likely change across seasons or years (Jang et al., 2019a). Such difficulty in detecting familiarity led Griffiths et al., (1999) to state that it is not possible to know an animal's previous experience within a given area even after running collecting behavioural observations for several years. However, animal's minds are dynamic systems in which new elements (e.g., feeding sites) are constantly incorporated while other elements are – adaptatively – forgotten (Tello-Ramos et al., 2019). Hence, it might be possible to detect how paths towards potentially novel feeding sites are optimised during an annual cycle with the accumulated number of visits, while controlling for potential cofounding variables (Janmaat, 2019).

In addition, individuals engage in conservative but potentially inefficient movement patterns to safeguard their internal energetic balance (Balaban-Feld et al., 2019). Arguably, individuals might only engage in flexible and efficient trajectories under conditions of increased energetic requirements (Bell, 1991; Janson & Byrne, 2007). The movement patterns of female moose (*Alces alces*) from Northern Sweden changed according to their reproductive status during the course of migration (Singh & Ericsson, 2014). Reproductive females, in addition to move faster than non-reproductive individuals, had higher chances of losing their calf if they were slow (Singh & Ericsson, 2014). Similarly, male African elephants in musth doubled their mean daily speed and travelled more than three times larger areas than non-musth males (Taylor et al., 2020). Taylor et al., (2020) argued that faster males had higher chances of reproductive success than slow males despite the high energetic costs derived from musth.

Hunger levels have also been described to drive movement patterns by modifying searching duration, resource selection and overall foraging effort (Bell,

1991). Gypsy moth (*Lymantia dispar*) larvae that were food deprived for longer than 24 hours after feeding on optimal food resources increased remarkably their travel speed and distance travelled but also increased the linearity of their searching paths (Wittman & Aukema, 2019). Cozzi et al., (2012) revealed that large predators in the Okavango Delta, Botswana, overlapped their temporal patterns at night likely driven by the possibility of starvation. Subdominant predators (wild African dogs, *Lycaon pictus*; cheetahs, *Acinonyx jubatus*) traded off the risk of encountering dominant predators (lions, *Panthera leo*; spotted hyenas, *Crocuta crocuta*) against the risk of starvation to increase their chances of foraging success by increasing their hunting behaviour at night (Cozzi et al., 2012).

Group living animals experience the additional challenge of asymmetrically sharing food resources upon arrival to the goal's location (Petit & Bon, 2010). Individuals that lead the group's movement likely benefit from greater control over the timing, distance and direction of the moves as well as preferential access to resources (Barelli et al., 2008; Strandburg-Peshkin et al., 2018). Female white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand, tended to consistently maintain the front position during travelling but only when they were in oestrus (i.e., reproductively cycling, Barelli et al., 2008). Thus, the increased energetic costs during oestrus periods were covered by arriving first at food resources and monopolising them in case fruit was scarce (Barelli et al., 2008). Likely, the larger an animal group is, the more advantageous it will be to gain prior access to food resources against within group competitors (Petit & Bon, 2010). Mbendjele hunter-gatherer women increased their travelling linearity when foraging in larger groups likely due to increased motivation to arrive at food locations earlier than the other group members (Jang et al., 2019a). Under periods of food scarcity such intragroup competition might increase since the value of

arriving earlier than other group members may even be crucial for survival (Singh & Ericsson, 2014). Therefore, both the energetic balance of the individual and the peer-pressure within the group for access to limited resources will likely shape the trajectories of animals while moving.

Inferring an individual or group's ability to navigate flexibly in space requires selecting specific measures that can be extracted from animals' trajectories (Janmaat, 2019). Increased linearity towards out of sight locations has been widely used in the study of animal navigation as indicative of spatial knowledge and movement flexibility (Benhamou, 2004; Janson & Byrne, 2007; Angilletta et al., 2008; Biro & Sasaki, 2017; Jang et al., 2019b). While route navigation has been argued to constrain animal's movement flexibility (Poucet, 1993), animals using route based navigation might still show the skills to increase travelling linearity when needed. If so, routes would likely be chosen as a conservative navigation mechanism to increase the chances of foraging success but animals will still possess the cognitive machinery necessary to engage in efficient and flexible movements (Byrne, 2000; Dolins & Mitchell, 2010). Nonhuman primates are especially flexible animals when solving socioecological problems by generating novel behavioural solutions or innovations (van Schaik, 2013). Such innovations are promoted within their social group through social learning in order to be established (Reader & Laland, 2002; van Schaik, 2013). For instance, chimpanzees at Bossou, Guinea, introduced innovations in their nut-cracking technique by either observing migrant individuals from other communities or through juveniles that were more willing to innovate (Boesch, 1994; Biro et al., 2003). Evidence in the literature highlights the variation in the ranging behaviour of primates under different ecological and social factors, suggesting that in addition to being socially flexible, some primate species may also be spatially flexible (Rosati, 2017; Tujague & Janson, 2018). For

instance, even though spider monkeys reportedly use routes to navigate (Di Fiore & Suarez, 2007), Valero & Byrne (2007) showed that spider monkeys in Yucatán, Mexico, travelled in highly linear paths constantly. Inconsistencies are also found in the opposite extent, where Western gorillas were shown to travel in non-linear paths despite of potentially using a coordinate based map (Salmi et al., 2020). Since even some closely related species show a clear distinction in their innovation repertoires in the context of sociality and cultural transmission (van Schaik et al., 2012), spatial behaviour may reflect such pattern as well.

Howler monkeys are able to engage in highly flexible dietary patterns under different environmental conditions (Diaz et al. 2010; Arroyo-Rodríguez et al. 2011) and can also adjust the length of their daily paths in periods of food shortage (Agostini et al., 2010; Fortes et al., 2015). Plante et al., (2014) described that howlers' satiation state (i.e., hunger levels) played a pivotal role when deciding their next travelling step. Similarly, increasing group size positively influenced the length of daily paths in *A. palliata*, which is the howler species that forms the largest groups and presents the widest variation in group size (Di Fiore et al., 2011). The relevance of experience was shown in black howlers in Belize: while established and translocated groups travelled similar daily path lengths, established groups showed more efficient patterns of home range use than translocated groups (Ostro et al., 1999). Likely, new groups need to increase their exploratory behaviour to gain similar spatiotemporal information of food resources than established groups before adjusting their ranging behaviour to more efficient patterns (Ostro et al., 1999). However, none of these studies have explored differences in the travelling trajectories associated with such factors.

Here, I aimed to determine whether black howlers increase the linearity of their travelling behaviour towards out of sight locations along an area continuously covered

by forest. First, I expected that under conditions of low food availability, black howlers would increase the linearity of their travelling trajectories. Second, I expected that linearity would increase with number of visits to revisited trees as a consequence of increasing experience or conditions. Third, I expected that black howlers would travel more linearly with increased hunger to fulfil their daily energetic requirements. Fourth, I expected that larger groups would travel more linearly than small groups under conditions of reduced food availability due to increasing intragroup competition (Fig. 5.2).

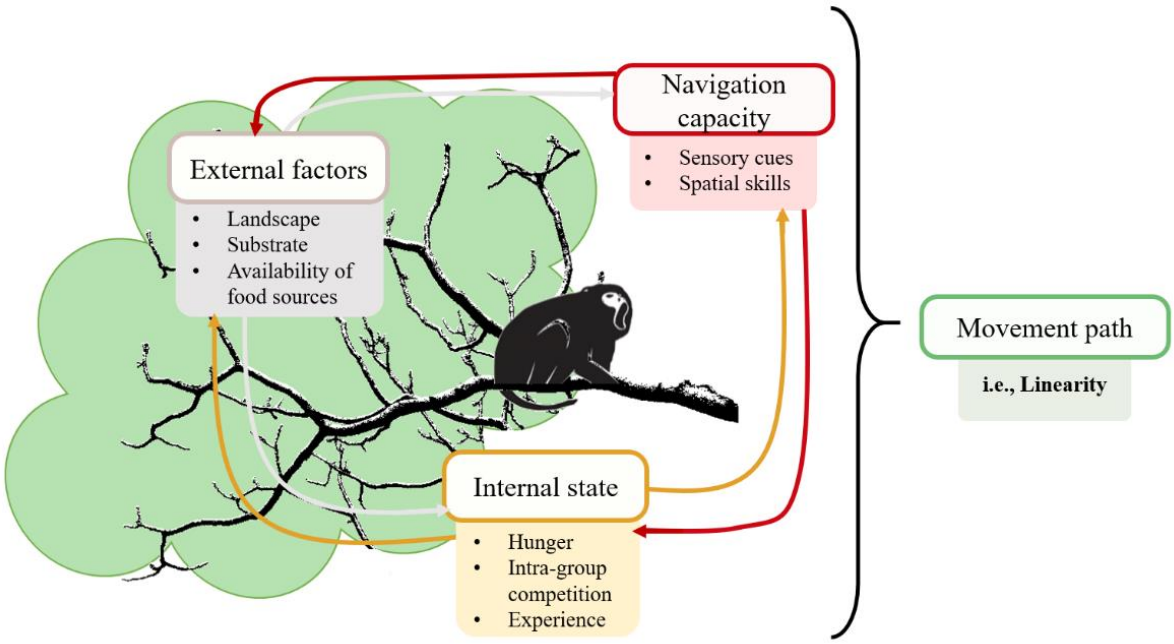


Figure 5. 2 Graphic illustration of the external and internal factors that are expected to influence the characteristics of black howlers' movement paths (i.e., linearity), design based on Nathan et al.'s, Movement Ecology Framework (2008).

5.2 Materials and Methods

5.2.1 Data Collection

See section 2.1 – 2.4.

5.2.2 Data analyses

I estimated plant phenological activity by calculating the Normalized Diversity Vegetation Index (hereafter NDVI; see section 2.4.5), which is the resultant coefficient between earth surface reflectance patterns in the red and near-infrared regions of the electromagnetic spectrum (Tucker, 1979; Willems et al., 2009):

$$NDVI = \frac{Band\ 5_{(NIR)} - Band\ 4_{(Red)}}{Band\ 5_{(NIR)} + Band\ 4_{(Red)}}$$

NDVI values range from -1 (absence of vegetation) to 1 (high photosynthetically active vegetation). I calculated monthly mean values for the home range of each study group and for PNP as a whole after correcting for cloud presence (Fig 5.3). I calculated these values for both TERRA (250 m reolution) and Landsat 8 (30 m resolution) images in order to compare them and select the most accurate set of images.

I measured "hunger" as the accumulated number of minutes that the group was observed feeding throughout the day (as in Plante et al., 2014). Therefore, I included in the analysis all previous feeding events in the same day, not only the last one, in order to account for the slow digestion rate of howlers (Milton, 1981; Plante et al., 2014).

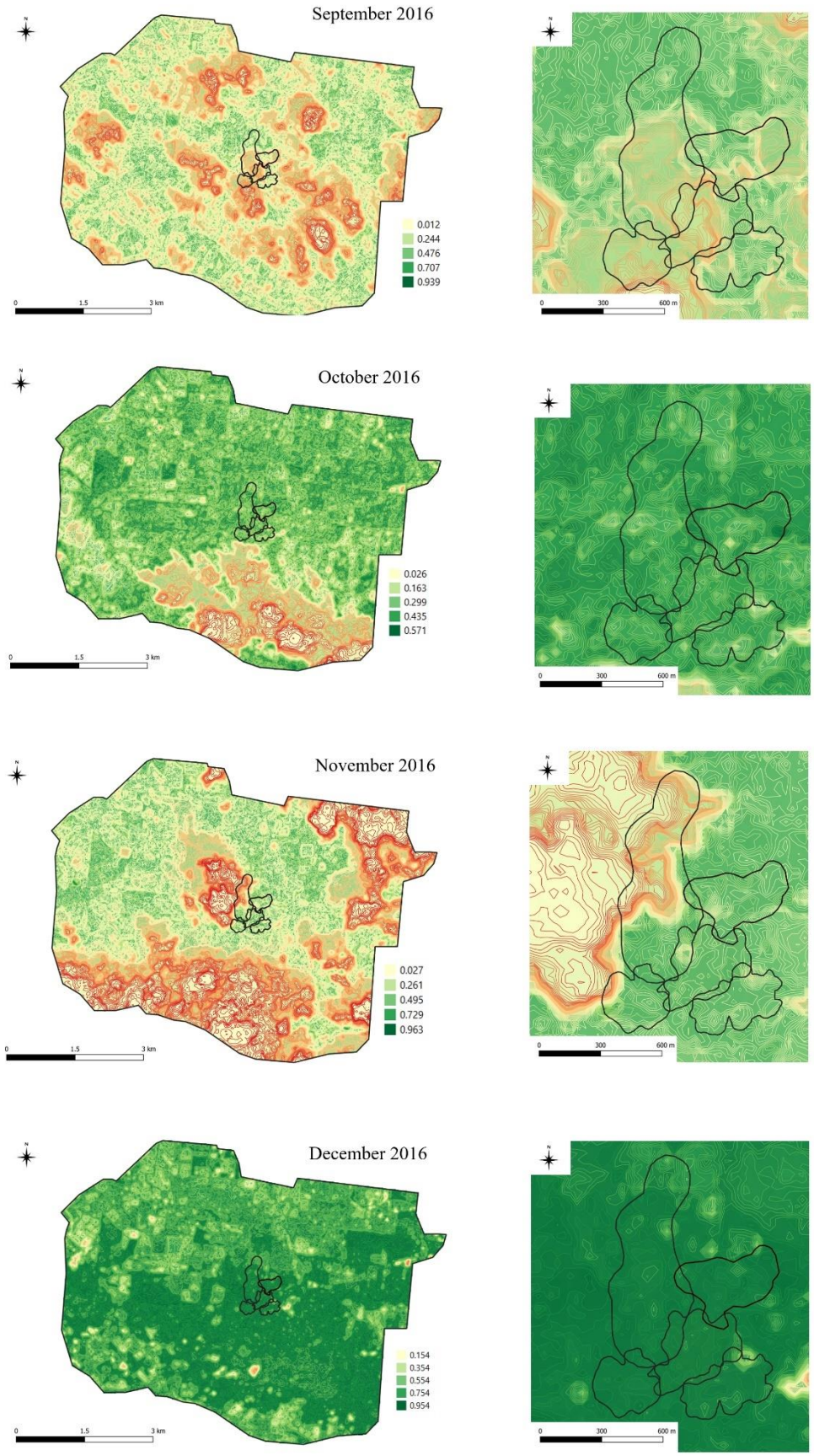


Figure 5. 3a Monthly NDVI values in PNP extracted from Landsat 8 (30 m resolution) from September 2016 to December 2016.

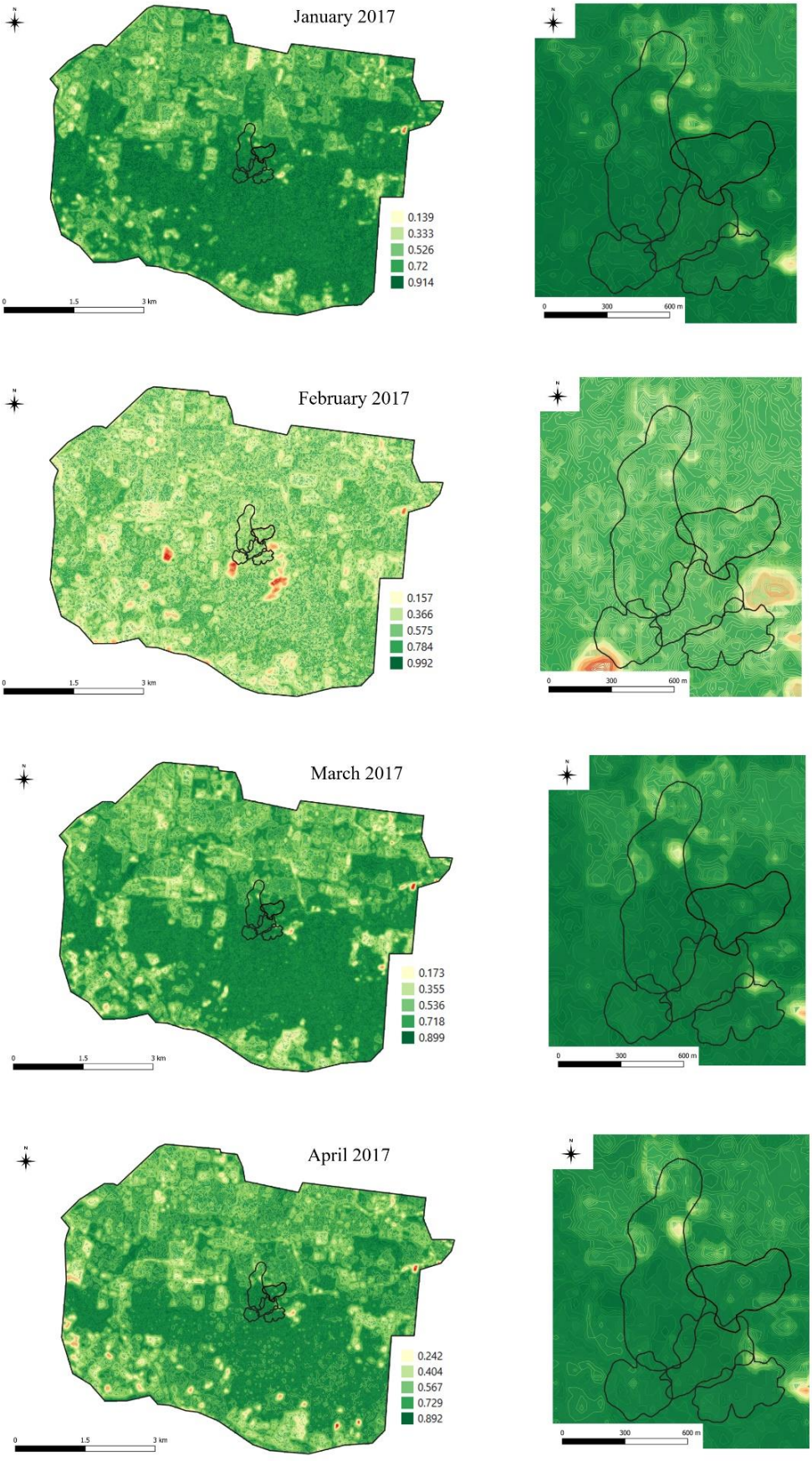


Figure 5.3b Monthly NDVI values in PNP extracted from Landsat 8 (30 m resolution) from January 2017 to April 2017.

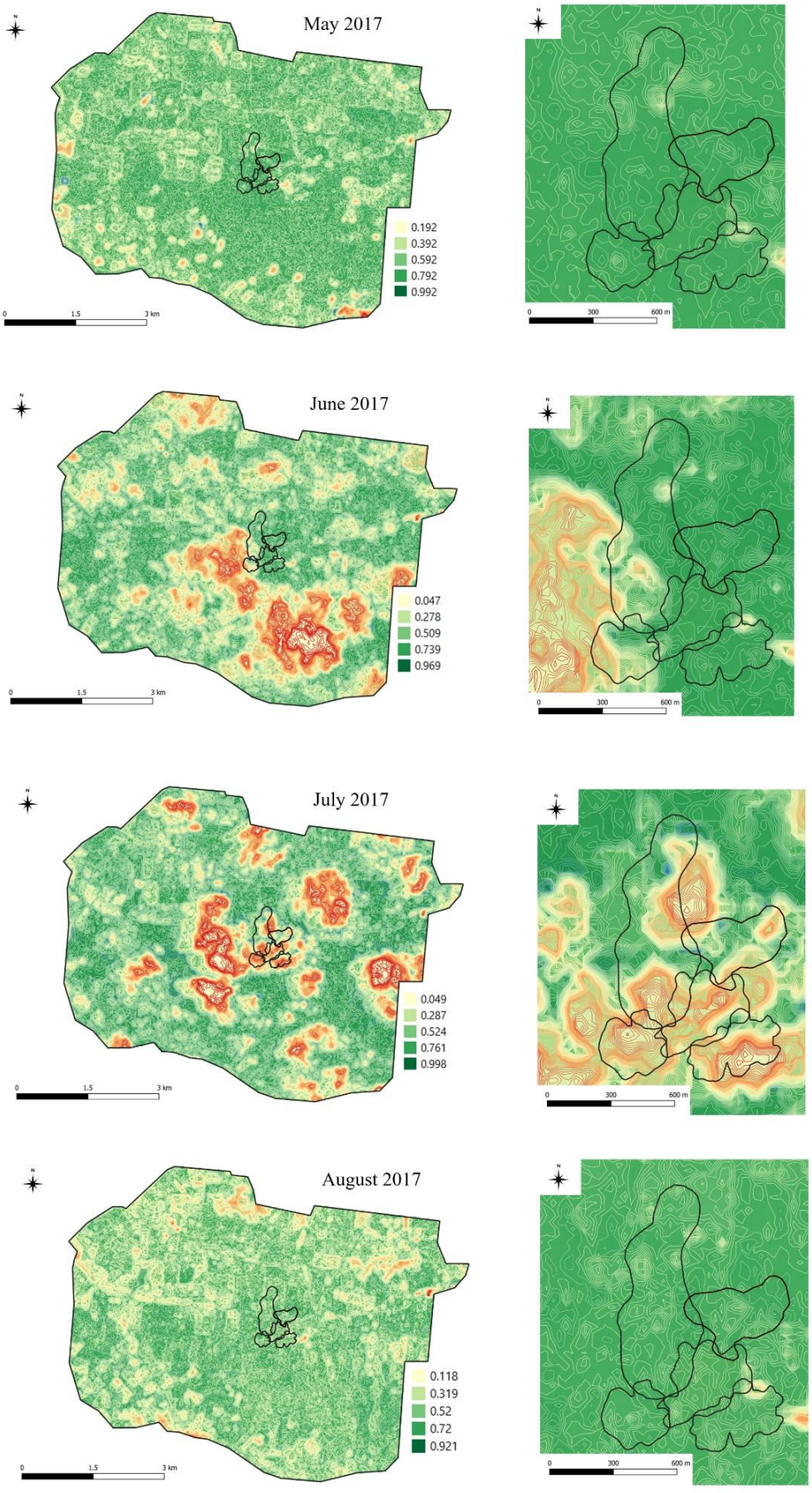
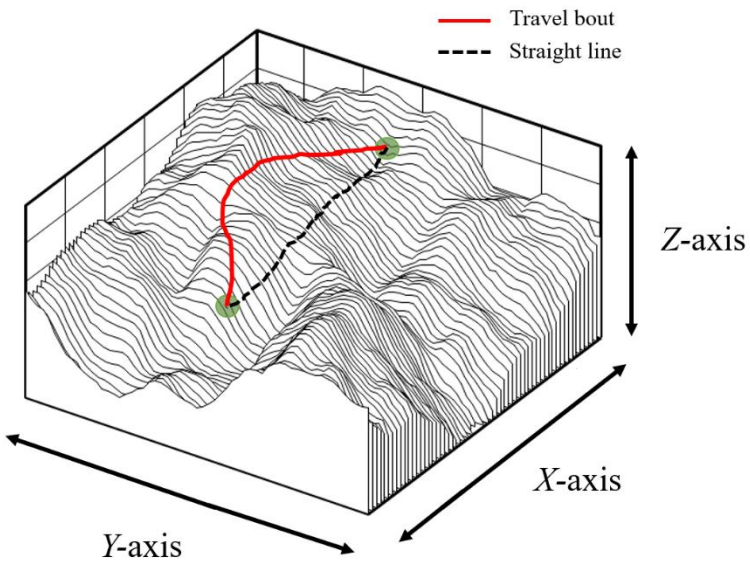


Figure 5.3c Monthly NDVI values in PNP extracted from Landsat 8 (30 m resolution) from May 2017 to August 2017.

I defined experience as the accumulated number of times that black howlers were observed to feed on, travel or rest at specific trees during the study period. The number of accumulated visits was measured independently for each group so that if two groups of black howlers visited the same tree within the same day, it would be considered as only one additional visit for each group. In addition, I estimated group size as the number of individuals present in the group at the moment of travelling, which included non-lactating infants, juveniles, subadults and adults.

I calculated linearity by dividing the actual performed distance between two locations by the straight line between these points (Valero & Byrne, 2007; Normand & Boesch, 2009; Jang et al. 2019a). When calculating both distances (i.e., the actual distance and the straightest path), I included difference in elevation as well as differences in the X and Y coordinates to account for PNP's terrain variability (Fig. 5.4).



$$linearity = \frac{Most\ direct\ distance\ A-B}{Actual\ distance\ performed\ A-B}$$

Figure 5. 4 Linearity calculated as the coefficient of the most straight line between two points (black dotted line) and the actual distance travelled (red line).

In order to control for the influence of visual cues in the linearity of the actual path, for statistical analyses, I selected travel bouts in which the straight line distance between the starting and ending location of the travel bout was longer than the visual detection distance. Since visual perception in howler monkeys has been described in between 35 – 38 metres (Milton, 1981; Hopkins, 2011), I selected a threshold of 40 m as the visual perception distance. Similarly, black howlers could be deviating their paths due to a lack of substrate availability to travel. Therefore, I selected those travel bouts that did not intercept a canopy gap within the estimated straight line in between the starting and ending point of the bout (i.e., travel bouts that occur throughout a continuous forest cover).

In addition, I calculated the proportion of each travel bout that fell within the route network. I created a 10 m buffer around habitual route segments that were used at least twice during the study period and calculated the length of each travel bout that fell within and outside such buffer. Subsequently, I calculated the coefficient between the length of the travel bout that fell within such buffer and the total length of such travel bout. I included this metric as a control in the statistical models in order to account for the potential influence of the route network's shape in the deviation rate – linearity – of black howlers.

4.2.5 Statistical Analyses

First, I evaluated differences in NDVI measures using Wilcoxon-signed rank testing for statistical differences: 1) between scales (250 m versus 30 m); and 2) between the study group's area and PNP. In addition, I ran two GLMMs using mean NDVI values at 250 m and 30 m resolution as response variables and month as predictor to test for seasonality. I include group ID as a random effect.

I designed a GLMM based on Jang et al., (2019b) with a beta error structure and logit link function, which I analysed using the function 'glmmTMB' from the R package "glmmTMB" (Brooks, 2017). The response variable was travel bout linearity excluding travel bouts shorter than howlers' visual detection distance and travel bouts that intercepted a canopy gap along their straight line. For the predictor variables, I included NDVI as a proxy for food availability, hunger as a proxy for internal motivation, number of accumulated visits as a proxy for experience and group size as a proxy for intragroup competition. In addition, I included two two-way interactions (i.e., NDVI * hunger; NDVI * group size) and a three-way interaction (i.e., NDVI * hunger * group size), since I hypothesised that the effects of food availability and internal motivation on linearity would interact with each other.

I controlled for straight line distance, the proportion of the travel bout that fell within the route network and the type of observed behaviour upon arrival at the goal location. Different goals can result in different foraging or searching strategies, which can influence howlers' travel linearity. Therefore, I categorised the arrival location into resting, loud calling and feeding. In addition, I included different categories within feeding specifying which food item was fed on at that moment (e.g., feeding on fruits, feeding on young leaves, feeding on mature leaves). I included random effects for the

identity of the group and observation and theoretically identifiable random slopes for the fixed effects within random intercepts.

5.3 Results

A Wilcoxon-signed rank test indicated that NDVI at 250 m resolution were statistically significantly higher than NDVI values at 30 m resolution ($Z = 1294.5$, p-value < 0.0001), suggesting an overestimation of photosynthesis activity at enlarged pixels (Fig. 5.5). I found statistical differences in NDVI values between the areas occupied by the study groups and the entire area of PNP both at 250 m resolution (mean PNP: 0.78 ± 0.09; mean study groups: 0.87 ± 0.02; $Z = 55$, p-value < 0.0001) and at 30 m resolution (mean PNP: 0.66 ± 0.11; mean study groups: 0.73 ± 0.04; $Z = 328.5$, p-value $= 0.027$).

I did not find significant differences in the NDVI values across months at 250 m resolution (likelihood ratio test: $\chi2 = 0.44$, d.f. $= 1$, p-value $= 0.507$) but found statistical differences at 30 m resolution (likelihood ratio test: $\chi2 = 14.68$, d.f. $= 1$, p-value < 0.001; Fig. 5.5, top). I found an increase in inter-monthly variation in NDVI values between November and December 2016, which was followed by a continuous decrease from February until August 2017 (Fig. 5.5, bottom).

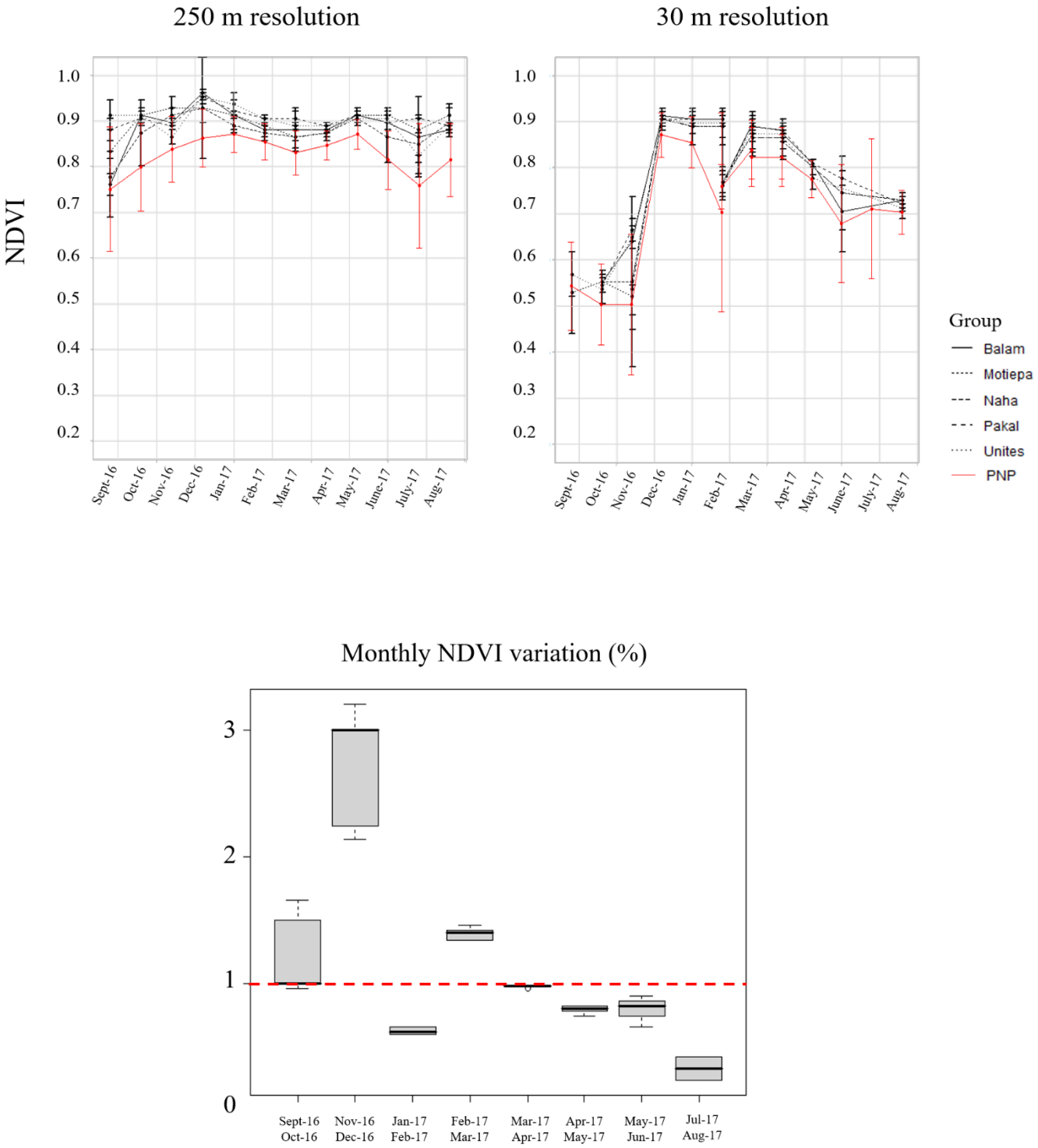


Figure 5. 5 Mean (±SD) NDVI values per month and study group (including the entire PNP) extracted from TERRA (250 m resolution) and Landsat 8 (30 m resolution) satellite imagery (top). Mean % NDVI variation among consecutive months (bottom).

Black howlers increased the number of visits to locations where they had been observed before on average 1.12 ± 0.24 times per month (mean number of revisits: September 2016 = 1.68 ± 1.08 visits per tree; August 2017 = 4.58 ± 3.91 visits per tree). Revisiting behaviour happened more often at fruiting FTs (4.37 ± 3.32 visits) and other FTs (3.06 ± 2.77 visits) than at loud calling (2.57 ± 2.30 visits) and resting (2.51 ± 2.05 visits) locations. Black howlers fed on average 198.53 ± 87.13 minutes during observation days. When testing for correlation between time spent feeding per day and mean NDVI values, I did not find a significant effect (r_s = -0.05, p-value = 0.197). Group size varied among observed groups (range: 4 – 11 individuals) but also within groups during the study period (mean variance in group size: 0.75 ± 0.3 individuals per group). Relative increases in group size occurred between the months of January and April following the local increase on mean NDVI values (Fig. 5.6).

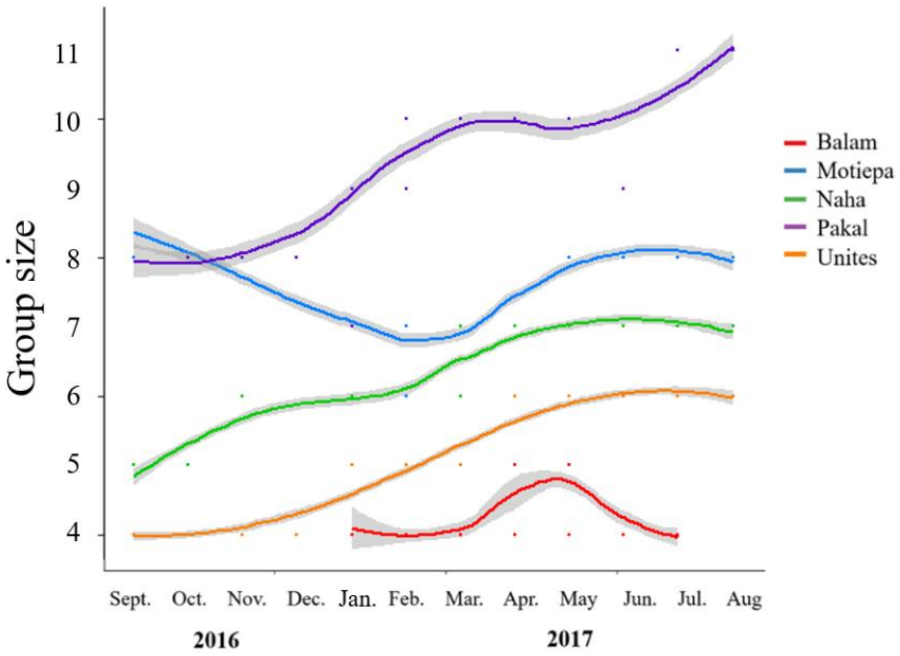


Figure 5. 6 Variability in black howlers' group size during the study period.

Linearity values did not differ among study groups ($H(4)$=5.32; p=0.26) and remained relatively constant throughout the study period (mean monthly range: 0.64 – 1.0; Fig. 5.7). I found that travel bouts shorter than black howlers' visual detection distance were statistically more linear than longer travel bouts ($H(5)$=301.75; p-value < 0.05; Table 5.1).

The comparison between the full and the null model showed that black howlers did not optimise the linearity of their trajectories as function of the predicted factors (likelihood ratio test: $\chi 2 = 3.52$, d.f. = 8, p-value = 0.898; Table 5.2).

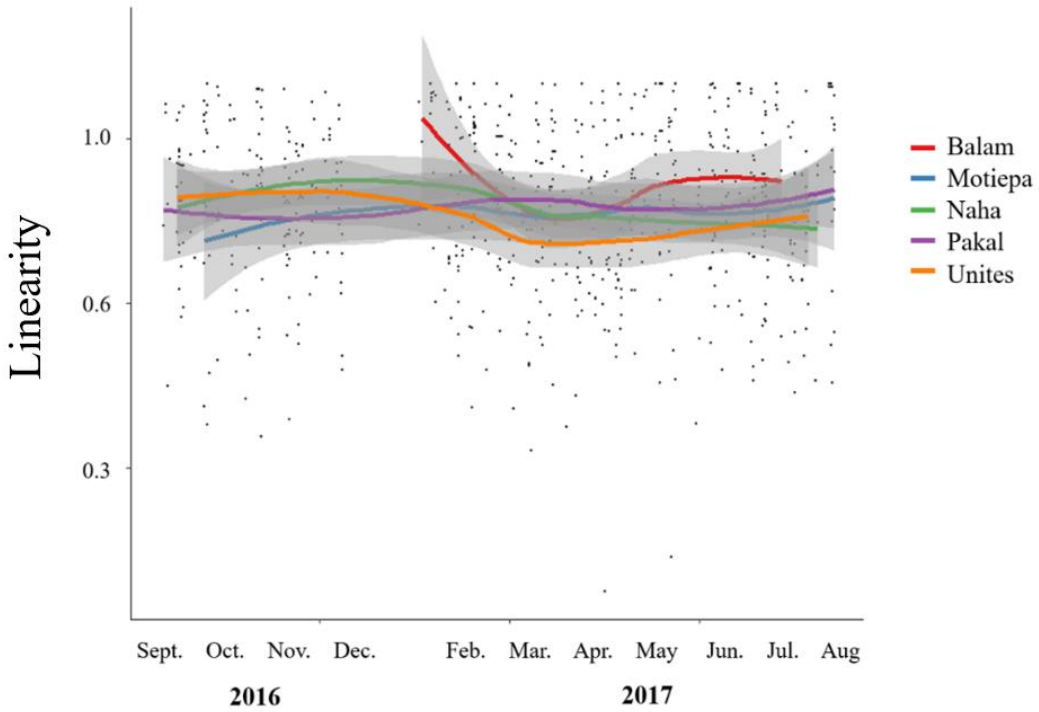


Figure 5. 7 Mean (±SD) linearity for travel bouts outside of the visual detection distance throughout the study period per study group.

Table 5. 1 Mean (±SD) linearity values for all recorded travel bout categorised by distance travelled.

Distance travelled (m)	Linearity	Sample size	% travel bouts deviated < 15%
0-40	0.85 ± 0.11	709	70.18
40-60	0.72 ± 0.17	304	14.27
60-80	0.69 ± 0.12	197	7.33
80-100	0.67 ± 0.11	152	3.47
100-120	0.68 ± 0.13	123	2.57
>120	0.64 ± 0.13	221	2.19

Table 5. 2 Results of the GLMM testing whether black howlers changed their travel linearity under different conditions.

Predictor variable	Estimate	SE	CI_{lower}	CI_{upper}	*p*-value
(Intercept)	1.549	0.196	[a]	[a]	[a]
NDVI	-0.019	0.059	-0.135	0.096	0.737
Accumulated number of visits	-0.044	0.036	-0.011	0.025	0.247
Hunger	-0.039	0.037	-0.114	0.035	0.286
Group size	-0.069	0.076	-0.218	0.079	0.349
NDVI * Group size	0.030	0.080	-0.126	0.186	0.703
NDVI * Hunger	0.021	0.035	-0.048	0.089	0.560
NDVI * Hunger * Group size	0.042	0.036	-0.029	0.113	0.249
Straight line distance [b]	-0.155	0.033	-0.219	-0.091	**< 0.001**
Proportion within route network [b]	-0.093	0.034	-0.159	-0.023	**0.006**
Behaviour upon arrival [b]	-0.511	0.225	-7.891	0.072	**0.010**

[a] Not shown because of having no meaningful or very limited interpretation.

[b] Represent control predictors included in the model

5.4 Discussion

Having explored the benefits derived from route based navigation, I aimed to focus on the potential constraint impose by moving throughout route networks. Since black howlers at PNP were able to benefit from monitoring food resources while avoiding canopy gaps by navigating through habitual routes, route navigation might have been an option rather than an imposition derived from a lack of cognitive power. Specifically, route based cognitive maps *per se* does not necessarily imply low cognitive skills. Therefore, I hypothesised that black howlers would optimise their spatial performance by increasing the linearity of their travelling trajectories when needed or required. Even though I found that black howlers travelled in a relatively linear fashion and experienced an annual variability of food resources, I did not find evidence to support the ability of black howlers to increase the linearity of their movement patterns under conditions of reduced food availability, increased experience or intragroup-competition.

Availability of food resources was expressed as the vegetation's photosynthetic activity mean values at a given moment – reported as the coefficient between reflected wavelengths in the red and near-infrared regions of the electromagnetic spectrum (Tucker, 1979). The use of remote sensing imagery to estimate the relationship between animals' distribution and movement patterns with vegetation activity has been well established during the last decades (Myneni et al., 1995) and proven to be effective both in savannahs (Willems et al., 2009) and rainforests (Cavada et al., 2017a,b). Here, I found that Landsat 8 revealed seasonal variability in vegetation characteristics at least during one annual cycle. A peak in rainfall was followed by a peak in vegetation activity, which led to a period of relative abundance in food resources and demographic increase in the observed groups of black howlers (Fig. 5.8). Subsequently, NDVI values

progressively decreased while rainfall increased by the end of the study period. Even though a validation of remote sensing imagery with field observations on tree phenological activity is still required to validate such estimations (Willems et al., 2009; Cavada et al., 2017a), these results fit into the overall framework of a cascade effect triggered by annual rainfall patterns. Yet, black howlers did not modify their travelling trajectories during periods of low food availability under which cognitive skills were expected to enhance howlers' foraging efficiency (Fagan et al., 2013). The fact that local increases in food availability run in parallel to relative increases in group size might indicate that black howlers would not need to modify their travel patterns to fulfil their energetic requirements. In addition, Amato & Righini, (2015) already showed that black howlers did not modify their activity patterns or diet under conditions of increased energetic or nutritional demands but presented a seasonal difference in microbiome composition. Changes in gut microbiome composition occurred among

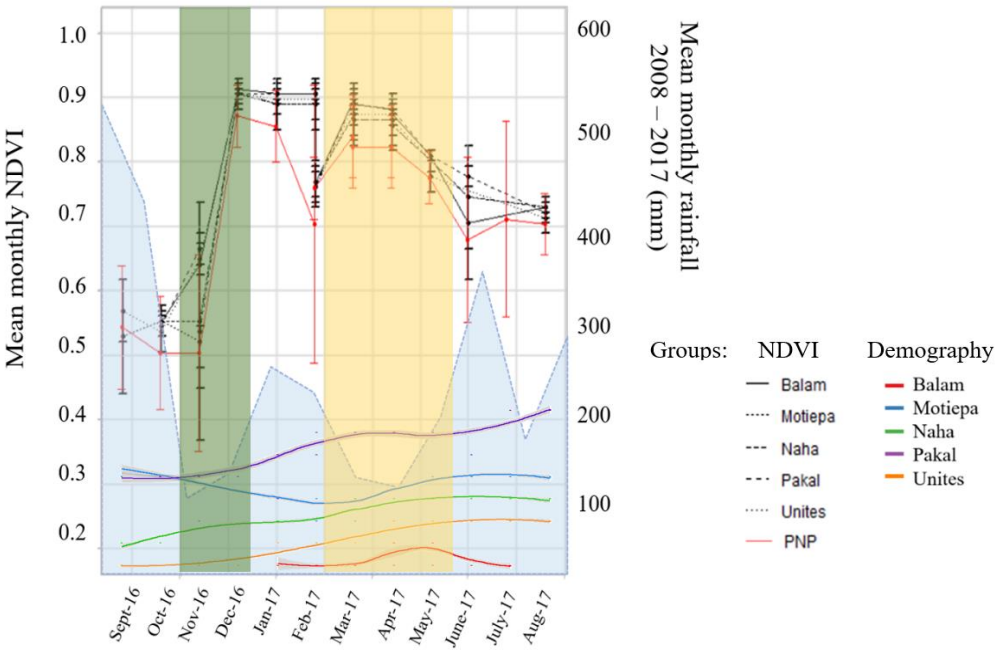


Figure. 5. 8 Time series plot describing variability in historical rainfall (CONAGUA,2019), mean monthly NDVI values and group size during the study period. Peak in NDVI values is highlighted in green and relative increase in demography is highlighted in yellow.

individuals and across seasons favouring the acquisition of energy according to each individual's needs (Amato & Garber, 2014; Amato, 2019; Righini et al., 2017). Therefore, black howlers may not be exposed to the energetic pressure of optimising their spatial performance under conditions of low food availability if their gut microbiomes can compensate for their energetic needs.

In addition, research on humans and mice have found a direct link between gut microbiome and cognitive flexibility (i.e., learning skills, memory), especially during development (Magnusson et al., 2015; Davidson et al., 2018). Individuals presenting a less-diverse microbiome showed poor memory capacity and low behavioural flexibility (Davidson, 2018). While microbiome composition can be flexible among individuals, the general trend in black howlers showed the opposite results: a species with a highly diverse gut microbiome did not show flexible spatial skills. This might be explained by a trade-off between cognitive flexibility and memory. Tello-Ramos et al., (2019) argued that retained memories may be favoured in stable environments over the acquisition of new information (i.e., cognitive flexibility) whereas rapidly changing environments may favour flexibility over retention. Despite the seasonal variability presented above, PNP is a relatively stable landscape where rapid changes do not typically occur. Black howlers' may engage in efficient navigation by memorising a series of habitual routes and specific locations while their foraging success may be compensated by changes in their gut microbiome. In the next following chapters, I will explore further aspects of black howlers' cognition related with planning abilities and memory and we will discuss its relationship with cognitive flexibility.

Contrary to my hypotheses, black howlers did not increase the linearity of their trajectories with accumulated number of visits to the same location. Increased experience did not play a role in shaping movement despite of previous evidence in

other animal taxa (Baddeley et al., 2012; Taylor et al., 2017; Jang et al., 2019a; Presotto et al., 2019) and humans (Byrne, 1979; Foo et al., 2005; Iachini, 2009). Arguably, the reduced home range of black howlers might imply that they are familiar to most of, if not their entire, home range. Contrary, there is a clear correlation between relative brain size and home range size within primate taxa, partially mediated by their gut systems (Barton 2000), which suggests that primates occupy territories according to their cognitive capacities and memory skills (Milton & May, 1976; Clutton-Brock & Harvey, 1980; Powell et al., 2017). Thus, even though black howlers occupy relatively small home ranges, they may not be able to remember of the environmental information within their home range leading to the existence of unfamiliar areas. In fact, there are areas within the black howlers' home ranges that were rarely visited during the study period (de Guinea, pers. obs.). Likely, the chances of discovering novel, unfamiliar resources decrease when following a fixed set of routes to navigate (Di Fiore & Suarez, 2007). Therefore, the temporal scale needed to detect an optimisation in ranging patterns towards newly found resources might be larger than the present study.

My results highlight that black howlers strongly rely on routes to navigate, even if it implies spending extra time and energy on travelling. Prioritising route navigation over flexible movements might be likely explained by cognitive constraints but also by interspecific differences in social behavioural flexibility (Dunbar & Shultz, 2007; Aureli et al., 2008; Manrique et al., 2013). Species that experience a constant change in the social context, which frequently form subgroups of variable size and composition throughout the day (i.e., spider monkeys, baboons, chimpanzees, etc.), may need high levels of behavioural flexibility (Aureli et al., 2008). Hence, flexibly switching among behavioural strategies depending on the subgroup composition may be especially beneficial for species with a high degree on fission-fusion dynamics (Amici et al., 2018;

Amici et al. 2008). For instance, Amici et al., (2018) tested whether different primate species were able to flexibly adapt their behavioural response in a task under different social contexts. Primate species with a high degree of fission-fusion dynamics (i.e., orangutans and spider monkeys) correctly processed variant social information and maximised the intake of food during the task outperforming species with a low degree of fission-fusion dynamics (i.e., gorillas and capuchins; Amici et al., 2018; see also Amici et al., 2008). Likely, behavioural flexibility derived from rapidly changing social dynamics may be reflected as well in the cognitive domain of spatial cognition (Burkart et al., 2017).

After comparing the mean linearity values reported in previous studies on primate navigation, I found that species with a high degree of fission-fusion dynamics showed highly linear travelling behaviour (Table 5.3). Conversely, species that travel cohesively within fixed social units showed an overall low travelling linearity. Therefore, cohesive species might rely increasingly more on routes to navigate, which typically deviate from the straight line, than fission-fusion species. Route navigation might facilitate intragroup coordination during travelling in highly cohesive species (Somveille et al., 2018; Sperber et al., 2019). Over prolonged periods of time this might be beneficial as well from optimising the shape and structure of the route network (Berdahl et al., 2018). Fission-fusion species might benefit from sophisticated cognitive skills that enable them to flexibly adjust their social behaviour and to process efficient navigation decisions under different contexts (Palacios-Romo et al., 2019). For instance, even though chimpanzees decreased their travelling linearity when travelling in larger groups (Jang et al., 2019a), they travelled in a highly linear manner when solitary and managed to adjust their travel speed according to the expected

Table 5. 3 Summary of mean linearity values reported in the literature in eight similar studies. Different biological traits that may explain primate's ability to engage in flexible movement patterns are reported as well per species.

Species	Linearity (mean ± SD)	Fission–fusion	% Fruits	Brain weight	Relative brain size	Tool use
Spider monkey *Ateles geoffroyi yucatanensis*	0.88 ± 0.03 [a]	Yes [b]	68.7 [c]	108.5 [c]	1.6 [c]	No
Baboons *Papio ursinus*	0.87 ± 0.03 [d]	No [e*]	87.0 [c]	195.4 [c]	0.9 [c]	No
Humans (Mbendjele) *Homo sapiens*	0.87 ± 0.05 [f]	Yes [f]	-	-	-	Yes [g]
Chimpanzees *Pan troglodytes*	0.85 ± 0.05 [f]	Yes [b]	63.0[c]	376.1[c]	0.8[c]	Yes [h]
Wedell's saddback tamarin *Saguinus fuscicollis*	0.68 ± 0.03 [i]	No [i]	60.4[c]	8.2[c]	2.0[c]	No
Black howler monkey *Alouatta pigra*	0.68 ± 0.07	No [j]	47.2[c]	53.0[c]	0.6[c]	No
Western gorillas *Gorilla gorilla*	0.64 ± 0.26 [k]	No [l]	67.0[c]	507.3[c]	0.4[c]	Yes [m]
Javan slow loris *Nycticebus javanicus*	0.61 ± 0.07 [n]	No [n]	60.0[c]	7.5[c]	< 0.01[c]	No
Black capuchin monkey *Sapajus nigritus*	0.57 ± 0.07 [o]	No [l]	67.5[c]	73.8[c]	2.6[c]	No

[a] Valero & Byrne, 2007; [b] Aureli et al., 2008; [c] DeCasien et al., 2017, Supplementary Material; [d] Noser & Byrne, 2014; [e] Lehman et al., 2007; [f] Jang et al., 2019a; [g] Lewis, 2002; [h] Inoue-Nakamura & Matsuzawa, 1997; [i] Porter & Garber, 2013; [j] Van Belle & Estrada, 2019; [k] Salmi et al., 2020; [l] Amici et al., 2008; [m]Fontaine et al., 1995; [n] Poindexter, 2017; [o] Presotto, 2009.

*The population studied by Noser & Byrne (2014) was cohesive but other baboon populations have been shown to engage in fission-fusion patterns (Aureli et al. 2008)

social and ecological context at their goal (Normand & Boesch, 2009; Janmaat et al., 2013).

Finally, the study of optimisation in spatial performance might require different approaches in animals with different navigation strategies. Travelling behaviour may not be optimised by increasing the linearity of movement trajectories in animals relying on route base navigation but combing habitual route segments in an optimal manner instead. By comparing different combinations of habitual route segments to navigate in between two locations within a route network against the chosen combination of segments, we might get insights not only on the animal's ability to optimise travelling trajectories but to plan such trajectories beforehand as well (Galloti et al., 2016; Teichroeb & Smeltzer, 2018).

Chapter 6: Goal-directed behaviour related with socioecological contexts: potential evidence for route planning in black howler monkeys.

6.1 Introduction

Mental representations of space, such as cognitive maps, provide a scaffold upon which an animal can structure the habitat wherein it lives (Behrens et al., 2018; Warren, 2019). Memories linked to specific locations provide an additional layer of information for animals to plan future actions and anticipate the occurrence of events across such cognitive maps (Gardner & Moser, 2017). Planning of movements is fundamentally supported by socioecological information gathered by individuals through interactions with their environment (Clayton, 2017). In the absence of such information, the emergence of planning abilities are prevented (Shettleworth, 2010). For instance, human patients unable to remember the past were also impaired in their ability to imagine the future despite having access to semantic knowledge of past and future (Rosenbaum et al., 2005). Hence, being able to recall particular events evolved in animals not for idle reminiscence about the past, but because it promotes adaptive action in the present and future (Shettleworth, 2010).

The storage and recalling of events derived from personal, unique experiences of individuals associated to specific locations in space and time is called episodic memory (Templer & Hampton, 2013). Until recently, humans were thought to be the only species with the cognitive capacity required to generate memories linked to contextual information (Suddendorf, 2013). However, in an array of species including Western scrub jays (*Aphelocoma coerulescens,* Clayton & Dickinson, 1998), chimpanzees (*Pan*

troglodytes, Martin-Ordas et al., 2010; but see Pladevall et al., 2020), rats (Crystal, 2016) and monkeys (*Lophocebus albigena*, grey-cheeked mangabeys, Janmaat et al. 2006; chacma baboons, Noser & Byrne 2015), multiple studies have highlighted the capacity of non-human animal species not only to plan when to return to specific locations but also to anticipate specific events taken place there (e.g., presence of food resources). Yet, there is a lack of understanding of which contextual factors trigger the generation of episodic memory in wild animal populations (Janmaat, 2019). Burkart et al., (2017) postulated that animal minds can be conceived as a collection of modules, each of which evolved to solve specific social and ecological adaptive problems, which combined contributed to the general intelligence of the species. The architecture of such modules might respond to evolutionary pressures experienced by a certain species over evolutionary time (Proulx et al., 2016). Exploring the ability of animals to recall specific social or ecological events will shed light on the architecture of cognitive modules and enhance our understanding on the relation between cognition and fitness (González-Gómez et al., 2011).

The primate radiation allows us to explore the evolution of different cognitive modules related to social and ecological contexts (Deaner et al., 2006). Primate sociality ranges from solitary individuals to large groups with multi-level societies, within-group friendships and coalitions, and cultural transmission of information (Zuberbühler & Byrne, 2006). In addition to the complexity of social contexts, ecological complexity has been proposed to better explain the evolution of brain size relative to body size across primates, where increasing level of frugivory requires advanced cognitive functions (DeCasien et al., 2017; González-Forero & Gardner, 2018). While primates' overall cognitive capacity resulted from the combination of ecological and social cognitive modules, each species is hypothesised to present specialised modules

according to their biological characteristics (Deaner et al., 2006; Amici et al., 2012; Burkart et al., 2017).

Infering the relative importance of social and ecological factors in the formation of episodic memory can be done by examining intentional revisits to specific locations (Clayton et al., 1998; Bracis et al., 2018; Noser & Byrne, 2015; Janson, 2019). The occurrence of biological events at the moment in time of the arrival can be interpreted as planning abilities derived from previous experiences of the animal at such revisited locations (Clayton et al., 1998; Bracis et al., 2018). While primate species that were highly exposed to social pressures during evolution might prioritise remembering social events, other primate species may favour remembering specific ecological events (Proulx et al., 2016). For instance, spider monkeys (*Ateles belzebuth*) in complex fission-fusion societies face the challenge of finding other members of their group after fissioning into subgroups (Sueur et al., 2011). Di Fiore & Suarez (2007) argued that spider monkeys remember "meeting locations" along frequently used routes, where fusion events are expected to take place among subgroups. On the other hand, the solitary, nocturnal mouse lemur (*Microcebus murinus*) approached out of sight locations where gum and honey had been present in a highly linear manner in comparison to other travel bouts performed that day (i.e., goal-directed movement; Joly & Zimmermann, 2011). Similar to gum and honey, fruits are ephemeral, energy-rich food resources which drive goal-directed behaviour in chimpanzees towards already visited feeding trees (Ban et al., 2014; 2016).

In fact, the spatiotemporal complexity of fruits in rainforests challenges primates' ability to remember foraging episodes at specific feeding trees and anticipate the emergence of fruits (Janmaat et al., 2016). Tree species' phenological cycles vary in synchrony, from all individual trees producing fruit within the same temporal period

annually to tree species in which each individual produces fruit within constrained temporal windows at irregular time intervals independently (Van Schaik et al., 1993; Chapman et al., 2003). Thus, while anticipating the presence of fruits at highly synchronous tree species requires memorising phenological cycles at species level, asynchronous species requires memorising at the individual tree level (Janmaat et al., 2012). Altogether, both the social and ecological complexity of the environment influence the experiences of individuals, which might selectively generate memories at specific locations depending on the benefits associated with anticipating different biological events for each species (Janson, 2019).

Inferring intentionality from movement patterns is challenging but current technological advances allow for detailed analyses of fine-resolution animal trajectories (Kays et al., 2015). Detecting directional changes in the trajectory of primates is a first step towards examining whether, and for how long. an individual has been heading into the direction of a target destination (Byrne et al., 2009; Potts et al., 2018). Directional changes indicate that, after arrival at a certain location, the individual potentially decided to head towards a new goal suggesting that the first location was the intended goal of the individual. Examining what biological meaningful events have taken place at locations (or goals) where an individual subsequently changes travel directions may shed light on the importance of different types of information that aids in generating memories (Byrne et al., 2009). Asensio et al., (2011) showed that white-handed gibbons (*Hylobates lar*) changed travel directions at preferred foraging tree species with fruits rather than other potential food resources. Thus, white-handed gibbons approached preferred feeding trees in a goal-directed manner when fruits were present, suggesting that gibbons were able to anticipate the presence of ephemeral food items. Further, gibbons did not show goal-directed behaviour towards locations where intergroup

encounters nor duets took place (Asensio et al., 2011). Indeed, there is a growing body of evidence highlighting primates' ability to approach key food resources in a goal-directed manner when ephemeral food items are present (Table 6.1). Yet, the role of

Table 6. 1 Summary of previous research using directional changes to infer planning abilities and episodic memory in different wild populations of primates. Social and ecological columns indicate whether the studies found evidence for planning abilities associated with social or ecological contexts.

Species	Family	Social	Ecological	Study
Mouse lemur (*Microcebus murinus*)	Cheirogaleidae		Yes	Joly & Zimmermann. 2011
White-faced saki monkey (*Pithecia pithecia*)	Pithecidae		No	Cunningham & Janson. 2013
Weddell's Saddleback tamarin (*Saguinus fuscicollis*)	Callitrichidae		Yes	Porter & Garber. 2013
Bearded capuchin monkey (*Sapajus libidinosus*)	Cebidae		Yes	Presotto et al.. 2018
Hamadryas baboon (*Papio hamadryas*)	Cercopithecidae		Yes	Schreier & Grove. 2014
Chacma baboon (*Papio ursinus*)	Cercopithecidae		Yes	Noser & Byrne 2014; De Raad & Hill. 2019
Sooty mangabeys (*Cercocebus atys*)	Cercopithecidae	Yes[1]		Neumann & Zuberbühler. 2016
White-handed gibbon (*Hylobates lar*)	Hylobatidae	No	Yes	Asensio et al.. 2011
Sumatran orangutan (*Pongo abelii*)	Hominidae		Yes	Hardus et al.. 2012; Bebko. 2018
Chimpanzee (*Pan troglodytes*)	Hominidae		Yes	Janmaat et al.. 2013; Ban et al.. 2014; Ban et al.. 2016

[1] Study showing that directional changes were linked to group coordination rather than planning abilities

social information on shaping the generation of episodic memories has been widely ignored despite the fact that primates likely remember locations related to fission and fusion events, extra-group copulations or intergroup encounters.

In addition to goal-directed travel, directional changes can also be driven by the structure of a primate's cognitive map and surrounding landscape. Primates that navigate using route networks systematically use nodes to make directional decisions (Bebko, 2018; Presotto et al., 2018). At nodes, additional information of the surroundings is perceived, typically via visual cues, leading to clusters of directional changes at specific locations (De Raad & Hill, 2019). Thus, nodes have been described at emergent trees (*Alouatta caraya*, Pereira, 2008), ridges (*Sapajus libidinosus*, Presotto et al., 2018) and associated with prominent landmarks in the horizon (*Papio hamadryas*, Sigg & Stolba, 1981; *Papio ursinus*, Noser & Byrne, 2014).

Similarly, the structure and resistance of the landscape can condition the shape of the route itself (Howard et al., 2015; 2019). Increasing the curvature of primate's trajectories at the same locations can lead to the misidentification of directional changes along routes (Presotto et al., 2018). For instance, bearded capuchinns (*Sapajus libidinosus*) preferred travelling through tree lines and traversable ridges performing *zig-zag* movements that increased the detection of directional changes along habitual routes (Presotto et al., 2018). Although the capuchins performed directional changes along routes, they returned to their previous heading direction shortly after, suggesting that directional changes resulted from the conditions of the landscape and not as a change in the travelling goal (Presotto et al., 2018). To correctly infer cognitive skills in wild populations, detection of directional changes might need to combine a description of the animal's navigation strategy together with an assessment of landscape properties (as discussed in Noser & Byrne, 2014).

The movement ecology of black howlers provides an ideal model to explore the socioecological context in which memories are generated to favour movement decisions (Milton, 1981; Hopkins, 2011; 2013; Van Belle et al., 2013a). Black howlers are constantly exposed to interacting with neighbouring groups with whom they tend to overlap their home ranges and engage in intergroup encounters (Van Belle et al., 2013b; Van Belle & Estrada, 2019). Intergroup encounters are characterised by the emission of loud calls (Kitchen, 2006) and loosing implies important costs such as denied access to key food resources (Van Belle et al., 2014). Hence, remembering the locations where previous intergroup encounters have taken place will likely enhance black howlers' ability to plan future travel bouts towards such locations.

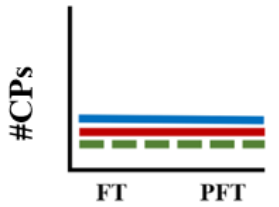
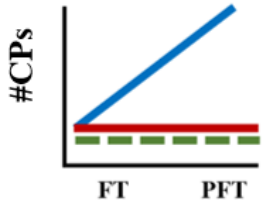
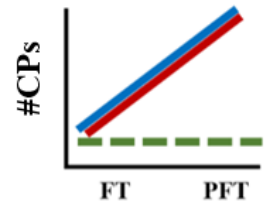
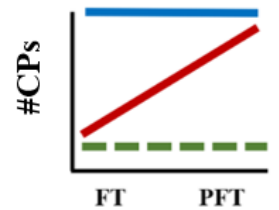
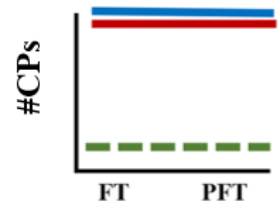
In addition, the emission of loud calls can occur spontaneously in the absence of intergroup encounters (Van Belle et al., 2013b). Van Belle & Estrada (2019) argue that black howlers engage in spontaneous loud calls as a spacing mechanism by which neighbouring groups inform each about their current location to make movement decisions. While the low frequency of black howler's calls favours the propagation of sound through rainforests (Naguib & Wiley, 2001; de Cunha et al., 2015), specific locations within their home range would likely improve even more the distance travelled by their calls rather than others (e.g., reduced physical barriers or foliage; Ramsier et al., 2019). Therefore, black howlers might intentionally return to locations where the emission of loud calls reached further distances enhancing their ability to communicate with neighbouring groups.

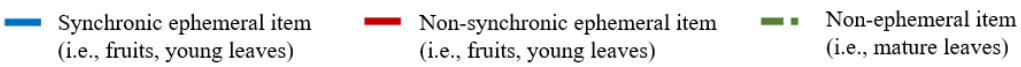
Additionally, black howlers' movement patterns have been shown to be strongly driven by the presence of fruits (Plante et al., 2014; Hopkins, 2016; but also flowers, Van Belle & Estrada, 2019). Anticipating the emergence of fruits at feeding trees would likely enhance black howler's accessibility to food resources against competitors and

facilitate the nutrient balance of their diets (Hopkins, 2016). While spatiotemporal knowledge of fruit production has already been shown in mantled howlers (Hopkins, 2016), further research is required to understand the process by which such information is processed as memories. An evaluation of the number of feeding trees with different levels of phenological synchrony that are approached intentionally during fruit bearing periods will shed light on the cognitive capacity of howler monkeys.

In the present chapter, I explored goal-directed behaviour in black howlers in relation to social and ecological events. I tested whether black howlers approached in a goal-directed manner locations where intergroup encounters and spontaneous loud calling bouts had taken place previously. In addition, I evaluated the importance of ecological contexts by examining goal-directed behaviour towards feeding trees. Specifically, I examined whether black howlers anticipate the emergence of food items at a small subset of preferred feeding trees or multiple individual trees. In parallel, I evaluated whether tree species synchrony influences the capacity of black howlers to anticipate the emergence of food items at specific locations. Both parameters are combined to test whether goal-directed behaviour in black howlers fits within a set of hypotheses with a varying degree of spatiotemporal ecological complexity (Table 6.2). Finally, I included terms to control for the role that structural factors and sensory cues have on the probability of finding a directional change in space. Although such predictors are explanatory for directional changes, they are indicative of the importance of visual cues and energy rather than planning abilities.

Table 6. 2 Summary of hypothesis testing whether black howler monkeys generate memories using ecological contexts. Graphs illustrate the number of directional changes ("#CPs") that occurred before or at locations where monkeys fed on different food items at the moment of arrival. The number of operative elements to be remembered is illustrated as FT (all potential feeding trees) and PFT (subset of preferred feeding trees). Spatiotemporal complexity and cognitive capacity (low-high) increase with each prediction.

Hypothesis	Spatiotemporal complexity of food resources incorporated into the cognitive process of generating memories
I. 	• No evidence for episodic memory nor goal-directed behaviour • Availability of food sources might be either too high or too low
II. 	• Memorization of few individual trees with highly phenological synchrony • Few spatial and temporal elements to memorize
III. 	• Memorization of few individual trees with both synchronous and asynchronous cycles • Focus on few spatial elements with more complex temporal cycles
IV. 	• Ability to remember multiple different locations with phenological synchrony • Linear increase in the number of spatial elements to memorize
V. 	• Memorization of multiple different phenological synchronies at individual level • Exponential increase in the temporal complexity memorized by the individual.



6.2 Methods

6.2.1 Data Collection

See section 2.1 – 2.4.

6.2.2 Data analysis

I identified directional changes (hereafter "change points" or "CPs") using the Change Point Test (hereafter "CPT", Byrne et al., 2009). Overall, the CPT evaluates whether the alignment of a previously determined number of vectors (q) before and after potential CPs along recorded travel paths statistically differs from the resultant length between the starting and ending point. I applied the CPT on 396 daily paths using q values between 2 and 7. I selected $q = 5$ based on the indications of Byrne et al., (2009) and set the alpha level at p-value < 0.05 ($N = 1000$, tolerance = 0.00002; Noser & Byrne, 2014). Post hoc, I determined the behaviour (i.e., travelling, feeding, loud calling) of the observed group of monkeys at the exact location and time that each CP was detected (Noser & Byrne., 2014).

I identified all directional changes that occurred either between travelling goals (i.e., CP occurred along a travel path) or at a travelling goal (i.e., loud calling and feeding locations). I defined a travel goal as a location in which at least two members of the group engaged in an activity other than travelling for a period longer than 5 min (i.e., resting, feeding, loud calling; following Van Belle et al., 2013b). CPs that occurred between travelling goals seemingly represent locations where travel decisions were made acting as an intermediate travel goal (Byrne et al., 2009). CPs that occurred at the location of the travel goal indicated a goal-directed approach to the location at which the change point occurred (Byrne et al., 2009; Asensio et al., 2011; Janmaat et al., 2013;

Ban et al., 2016). I included both types of CPs (i.e., CPs along travel bouts and at the end of travel bouts) in the statistical analyses to maximise the sample size and enhance the power of the analyses (Ban et al., 2016). Overall, goal-directedness was defined as a prolonged linear travel towards a specific location succeed by a significant change in direction.

I assessed whether a group had already experienced an intergroup encounter (hereafter IGE) at the location they were observed loud calling by overlapping the locations where all previous IGE events occurred and tracing a circle of 15 m radius from the current loud calling location. If at least one IGE had taken place within the circle, I determined that the group had experienced an IGE at that location previously (Fig. 6.2). I selected a 15 m radius based on: 1) the estimated GPS error of the tracking devices (6.6 ± SD 2.3 m); 2) the estimated average spread of the group (*ca.* 15 m; Van Belle & Estrada., 2019); and, 3) the potential movement of the observed group in any direction from one tree to another during the encounter. Because I was interested in the trajectory that led to the location where loud calling happened (Van Belle et al., 2013b), if two or more loud calling bouts occurred consecutively at the same site with no travelling in between, I incorporated only the first loud calling bout into the analyses.

To infer the phenological synchrony level of each tree species, SVB calculated the simultaneous production of fruits and young leaves in individual trees of the same species at regular time intervals (Janmaat et al., 2013). For this, SVB calculated the Spearman rank correlation coefficients between all pairs of individual feeding trees of the species in which the monkeys were observed to feed on young leaves or fruits. Finally, we calculated the average among all the correlation coefficients for young leaves and fruits regardless of each other (Bjørnstad et al., 1999; Marshall & Burguess, 2015). While low mean correlation values indicate that individual trees of the same

species did not synchronize the production of specific items (i.e., young leaves. fruits) during the study period, high mean correlation values point out tree species that synchronized the production of such items. Additionally, I classified preferred FTs for each group separately as feeding locations that made up at least 1% of the overall time spent feeding by that group during the study period (Asensio et al., 2011).

I controlled for the potential influence of the structure of the route network and the landscape in the detection of CPs by incorporating the following variables in the models. First, I calculated whether each observed feeding and loud calling bout fell within a 15 m diameter of the intersections (N = 113) among at least two habitual route segments to control for an overestimation of CPs at nodes (Presotto et al., 2018). Second, I determined whether CPs located along habitual route segments concurred within 15 m of at least another CP to control for the potential influence of the habitual route's curvature in the detection of CPs. Third, I calculated the maximum rate of change in elevation for each quadrat relative to its adjacent quadrats to include a metric control for slope in the model (as in Chapter 4; Presotto et al., 2018). Finally, I also controlled for the influence of sensory cues (i.e., olfaction, vision), which could influence the movement decisions of black howlers when travelling to feed at specific locations, by calculating travelling distance from the previous stop. The larger the distance, the lower the potential influence of sensory cues in the decisions of black howlers when approaching specific locations in a goal-directed manner to feed.

6.2.3 Statistical Analyses

I designed one GLMM to analyse the social aspect (loud calling) of goal-directed behaviour and three further GLMMs to analyse the ecological aspects (feeding) of goal-directed behaviour. For all models, I included predictors to control for route network structure (i.e., proximity to route's intersections, frequency of route's use) and landscape structure (i.e., slope). For the social model, I also included a control predictor for internal motivation of the group to reach a goal (i.e., duration of the loud calling bout). For the ecological models, I controlled for the potential influence of sensory cues in the goal-directed behaviour of black howlers when approaching specific locations to feed (i.e., distance from starting location to CP). Finally, I accounted for potential differences among groups by including group ID as a random variable (random intercept) in all models.

In the social model, the response variable was presence/absence of significant directional changes both before and at loud calling locations. The predictor variables were loud calling context (i.e., occurrence or absence of IGE at the moment of engaging in loud calls), overlapping area, occurrence of previous IGE at that location and accumulated previous number of visits to that location to engage in loud calls. I included an interaction between overlapping area and context because I predicted that howler monkeys would approach overlapping areas in a goal-directed manner because they would anticipate the occurrence of IGEs: [social model: $CP_{loud\ calling}$ ~ loud calling context * overlapping area + previous IGE + accumulated visits to howl + loud calling duration + intersection + route's curvature + slope + (1 | group ID)].

Subsequently, I fitted three additional models using presence/absence of significant directional changes before and at feeding locations in which I also included

tree ID as random effect variable. First, I tested whether the probability of detecting a directional change varied as a function of the item the monkeys fed on (i.e., mature leaves, young leaves, fruits) at the goal location [ecological model 1: $CP_{feeding}$ ~ item fed on + intersection + route's curvature + slope + distance from previous stop + (1 | group ID) + (1 | tree ID)]. Second, I tested whether the probability of approaching locations in a goal-directed manner to feed on young leaves changed as a function of the synchrony level of the tree species and the preference shown towards that specific tree [ecological model 2: $CP_{young\ leaves}$ ~ synchrony * tree preference + intersection + route's curvature + slope + distance from previous stop + (1 | group ID) + (1 | tree ID)]. Third, I fitted the same model for fruit consumption [ecological model 3: CP_{fruits} ~ synchrony * tree preference + intersection + route's curvature + slope + distance from previous stop + (1 | group ID) + (1 | tree ID)].

6.3 Results

I detected 318 change points for the travel trajectories of five black howler groups (mean per group: 64.4 change points ± SD 22.5, Table 6.3). Of these, 136 directional changes took place at the goal of the travelling bout (Case 1 in Fig. 6.1), of which 20 (15.3%) concurred with loud calling bouts and 81 (62.8%) concurred with feeding bouts. In addition, I detected that 187 directional changes occurred before reaching a goal (i.e., in between travelling goals; Case 2 in Fig. 6.1), of which 26 change points (14%) were associated with loud calling bouts and 117 change points (62.5%) were associated with feeding bouts.

We recorded 454 loud calling bouts (mean per group: 90.8 ± SD 26.9) indicating that black howler monkeys engaged on 1.52 ± 0.44 SD loud calling bouts per observational day during the study period. Of these bouts, 115 were within an IGE context and 339 were spontaneous or in response to neighbouring calls. Loud calling bouts that occurred within overlap zones with neighbouring groups were associated to directional changes in 23.9% of the cases, of which 64.6% were IGE and 36.6% were spontaneous loud calls.

Table 6. 3 Sample size of the detected number of CPs associated with feeding bouts[1] and loud calling bouts[2], and accumulated number of recorded feeding and loud calling bouts per study group.

Group	N CPs	N Feeding bouts	N Loud calling bouts	$CP_{ecological}$[1]		CP_{social}[2]	
				at	before	at	Before
Balam	70	161	83	8	14	6	3
Motiepa	60	233	56	15	15	3	5
Naha	100	252	79	13	30	3	9
Pakal	42	216	121	10	11	5	4
Unites	50	172	115	12	13	4	5

We recorded 1034 feeding bouts (mean per group: 206.8 ± SD 39.1, Table 6.3) in 523 individual FTs of 38 tree species. Thus, black howler monkeys at PNP engaged in 3.45 ± SD 0.58 feeding bouts per observation day. We found that 55.9 % of directional changes associated with feeding bouts were associated to fruit consumption, while 33.8 % and 10.3 % were associated to young leaf and mature leaf consumption respectively. We determined 26.6 ± SD 3.4 preferred FTs per study group out of a total of 1830 marked FTs.

For 31 fruit tree species and 19 young leaf tree species, we estimated phenological synchrony in between 7 – 266 individual trees from each species (mean: $N_{fruit\ tree}$: 31.1 ± 50.3 trees; $N_{young\ leaf}$: 29.6 ± 38.5 trees). Mean fruit tree synchrony was estimated as 0.29 ± SD 0.18 and ranged between 0.05 (*Ficus insipida*) to 0.71 (*Spondias radlkoferii*). Similarly, young leaf synchrony was estimated as 0.31 ± SD 0.26 and ranged between 0.03 (*Ficus pertusa*) to 0.80 (*Acacia glomerosa*). All trees belonging to *Ficus spp*. showed mean fruit (0.14 ± SD 0.10) and young leaf (0.10 ± SD 0.09) synchrony values below the average mean synchrony values. The mean synchrony values for preferred fruit trees was 0.18 ± SD 0.16 and 0.35 ± SD 0.25 for non preferred fruit trees, while the mean synchrony values for young leaf trees was 0.16 ± SD 0.12 for preferred trees and 0.27 ± SD 0.17 for non preferred trees.

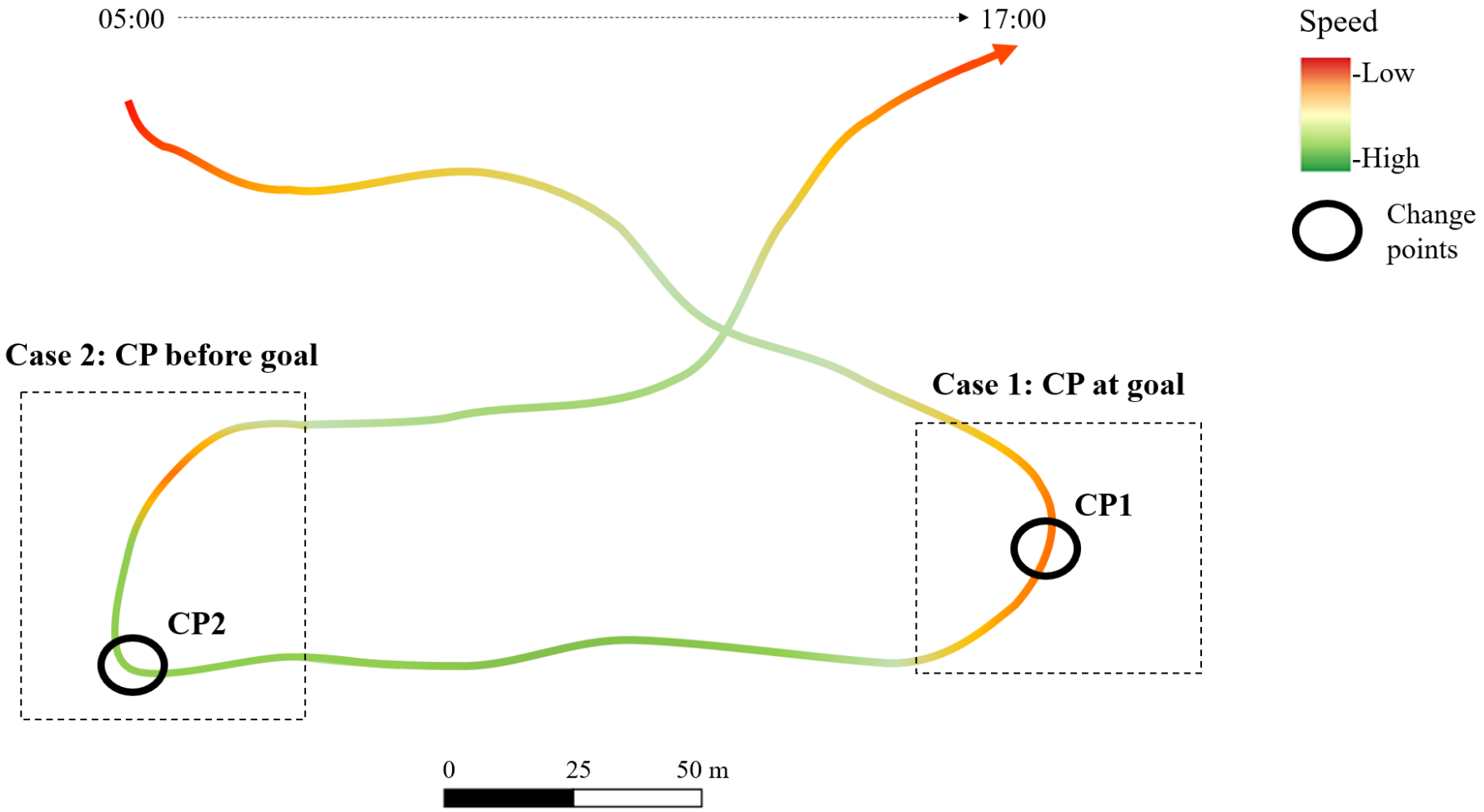


Figure 6. 1 Illustrative example showing the location of CPs along a daily path of black howlers that happened: a) Case 1: at goal locations where the group engaged in an activity other than traveling for more than five minutes (i.e., feeding, loud calling); and, b) Case 2: while travelling before reaching a location where a feeding or loud calling bout occurred. In this example, speed is shown in a coloured gradient in which red indicates locations where the group stopped.

Influence of social events in the detection of CP

The comparison between the full and null social models revealed that there were statistically significant differences in the probability of detecting a directional change at specific locations where loud calling bouts took place (social model, likelihood ratio test: $\chi^2 = 14.12$, d.f. = 5, p-value = 0.015). I found that black howlers were more likely to approach a loud calling location in a goal-directed manner when an IGE had taken place at that location and with the accumulated number of times that they were observed engaging in loud calls at that specific location (Fig. 6.2; Table 6.4). Thus, the probability of approaching a loud calling location in a goal-directed manner increased 3.32 ± 2.19 SD times if at least one IGE had taken place at that location before and 1.24 ± 0.69 SD times with the accumulated number of loud calling events that had taken place previously at that location. I found no effect from the other predictors in the model (Table 6.4).

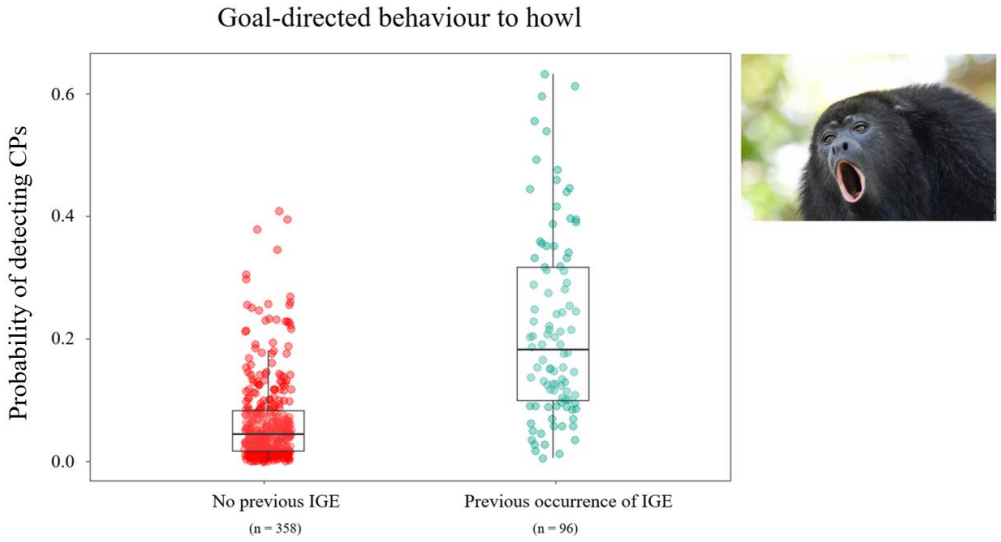


Figure 6. 2 Probability of detecting a directional change before and at locations where black howler monkeys engaged in loud calling bouts when IGE did not occur prior to the observed directional change; and. when IGE occurred at least once prior the observed directional change.

Table 6. 4 Results of the social GLMM testing whether black howler monkeys approached specific locations to engage in loud calling bouts in a goal directed manner.

Predictor variable	Estimate	SE	CI_{lower}	CI_{upper}	*p*-value
(Intercept)	-3.592	0.699	-4.963	-2.222	[a]
Context	-0.435	0.610	-1.631	0.760	0.475
Overlapping area	0.755	0.590	-0.401	1.910	0.201
Times loud calling at that location before	0.433	0.230	-0.018	0.883	0.062
Previous IGE experience	**1.609**	**0.574**	**0.484**	**2.735**	**0.005**
Context * Overlap area	0.116	1.144	-2.126	2.359	0.919
Duration of loud calling bout[b]	0.173	0.252	-0.320	0.666	0.491
Intersection [b]	-2.197	2.889	-7.860	3.466	0.447
Slope [b]	-0.136	0.279	-0.683	0.411	0.626
Route's curvature [b]	0.197	0.935	-1.635	2.029	0.833

[a] Not shown because of having no meaningful or very limited interpretation.

[b] Represent control predictors included in the model

Influence of feeding events in the detection of CP

I found that food item type influenced the goal-directed behaviour of black howler monkeys towards feeding sites (ecological model 1, likelihood ration test: χ^2 = 7.3, d.f.= 2, *p*-value = 0.026; Table 6.5). Black howlers were more likely to approach a specific feeding site in a goal-directed manner to feed on fruits rather than to feed on young leaves or mature leaves (mature leaves: mean 0.07 ± SD 0.07; young leaves: 0.10 ± SD 0.03; fruits: mean 0.19 ± SD 0.04; Fig. 6.3).

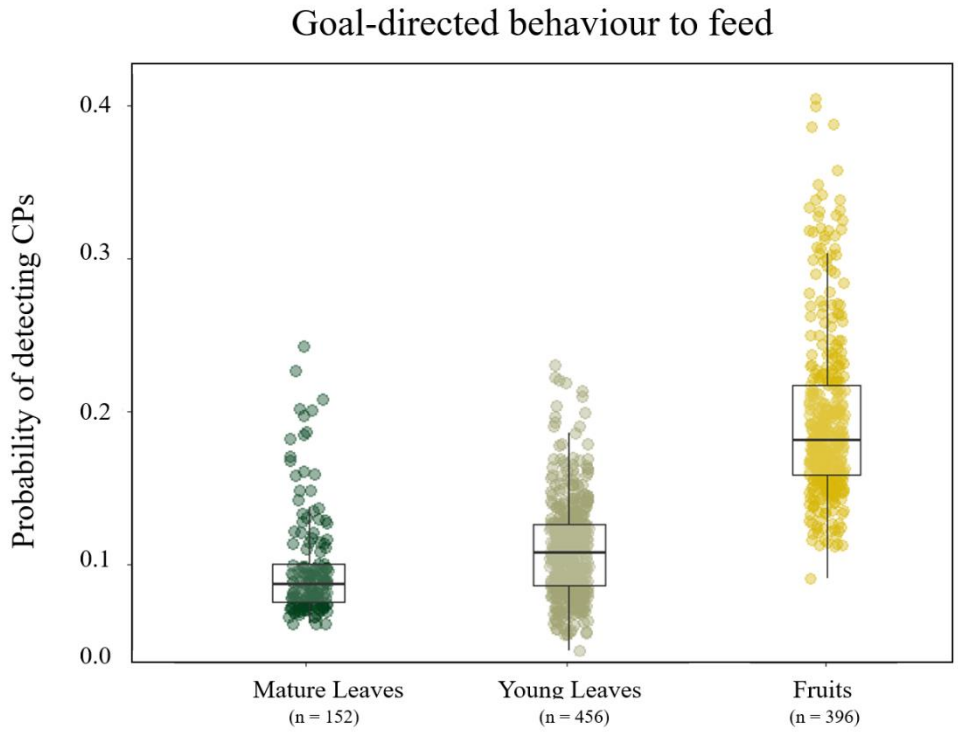


Figure 6. 3 Probability of approaching feeding sites in a goal-directed manner as a function of the item fed at that site.

Table 6. 5 Results of the ecological model 1 testing the influence of food type in the goal-directed behaviour of black howlers.

Predictor variable	Estimate	SE	CI_{lower}	CI_{upper}	*p*-value
(Intercept)	-1.460	0.158	-1.77	-1.149	
Item type	**8.561**	**0.289**	**-1.446**	**-0.158**	**0.013**
Intersection [b]	0.003	0.211	-0.411	0.418	0.988
Slope [b]	0.147	0.115	-0.058	0.353	0.156
Route's curvature [b]	-0.016	0.106	-0.223	0.191	0.882
Distance from previous stop [b]	0.175	0.110	-0.041	0.391	0.227

[a] Not shown because of having no meaningful or very limited interpretation.

[b] Represent control predictors included in the model

I did not find an influence in tree phenological synchrony nor FT preference for the probability of detecting a directional change at feeding sites of young leaves (ecological model 2, likelihood ration test: $\chi^2 = 5.0$, d.f. = 3, *p*-value = 0.172; Table 6.6). Contrarily, I found that the same model structure for fruits significantly differed from the null model (ecological model 3, likelihood-ratio test: $\chi^2 = 9.19$, d.f. = 3, *p*-value = 0.027; Table 6.6). Black howlers increased the likelihood of approaching FTs in a goal directed manner to feed on fruits at preferred FTs but only when these FTs presented a synchronous phenology (Table 6.6; Fig. 6.4).

Table 6. 6 Results of the ecological models 3 and 4 testing whether black howlers approached specific feeding sites in a goal-directed manner depending on the characteristics of the feeding tree (preference and level of synchrony).

Response variable	**Probability of performing a directional change at young leaves feeding sites**				
Full null model comparison	$\chi2$ = 5.03. d.f. = 3, *p*-value = 0.171				
Predictor variable	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	***p*-value**
(Intercept)	-2.096	0.217	-2.522	-1.671	[a]
Synchrony	-0.330	0.202	-0.725	0.064	0.077
Preferred tree	-0.695	0.734	-2.133	0.743	0.223
Synchrony * Preferred tree	-0.649	0.697	-2.015	0.717	0.329
Intersection [b]	-0.029	0.365	-0.743	0.686	0.937
Slope [b]	-0.203	0.185	-0.565	0.159	0.245
Route's curvature [b]	-0.130	0.204	-0.529	0.269	0.557
Distance from previous stop [b]	-0.087	0.163	-0.407	0.232	0.595
Response variable	**Probability of performing a directional change at fruit feeding sites**				
Full null model comparison	$\chi2$ = 9.19. d.f. = 3, ***p*-value = 0.027**				
Predictor variable	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	***p*-value**
(Intercept)	-1.851	0.356	-2.547	-1.153	[a]
Synchrony	0.212	0.221	-0.221	0.644	0.337
Preferred tree	**0.869**	**0.374**	**0.136**	**1.602**	**0.020**
Synchrony * Preferred tree	**0.879**	**0.345**	**0.203**	**1.555**	**0.011**
Intersection [b]	-0.174	0.299	-0.76	0.411	0.56
Slope [b]	0.238	0.175	-0.105	0.581	0.173
Route's curvature [b]	0.051	0.149	-0.242	0.344	0.734
Distance from previous stop [b]	**0.343**	**0.166**	**0.017**	**0.668**	**0.039**

[a] Not shown because of having no meaningful or very limited interpretation.

[b] Represent control predictors included in the model

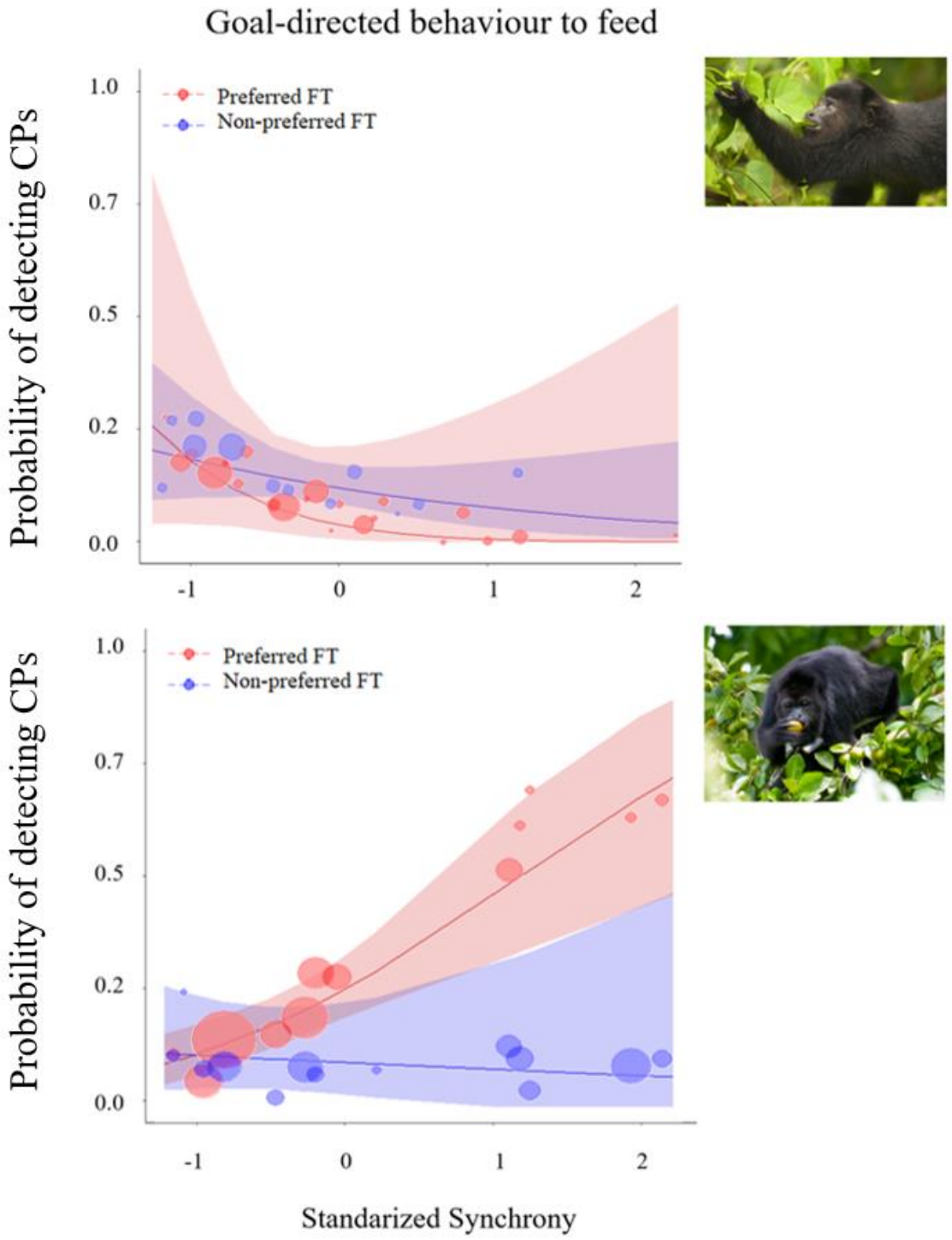


Figure 6. 4 Probability of detecting a change point (CPs) before and at locations where black howlers engaged on feeding bouts. I found that black howlers did not approach locations to feed on young leaves in a goal-directed manner either to reach preferred FTs nor synchronous tree species (top); and, black howlers approached preferred FTs to feed on fruits in a goal directed manner only when the FTs had phenological synchrony (bottom).

6.4 Discussion

These findings indicate that biologically meaningful events were associated with significant directional changes in black howlers at Palenque National Park. After having experienced encounters with neighbouring groups at specific locations, black howlers were more likely to return to these locations in a goal-directed manner to engage in loud calling bouts. Such likelihood also increased with the number of times the observed group had engaged in loud callings at that location before. Similarly, black howlers were shown to approach feeding locations in a goal-directed manner where fruits were present rather than young or mature leaves. Yet, goal-directed behaviour towards fruiting trees was limited to preferred individual trees with phenological synchrony. Overall, experiencing social and ecological events likely shapes black howlers' travelling trajectories reflecting potential planning abilities towards relevant locations.

The role of social information in planning abilities has been rarely documented in primates, whose decisions has been described to be mainly influenced by ecological events (Asensio et al., 2011; Cunningham & Janson, 2013; Janmaat et al., 2014; Hopkins, 2016). I found novel evidence linking past social events and movement decision-making in wild primate populations. Black howlers were shown to intentionally approach specific sites to engage in loud calling bouts only after intergroup encounters with neighbouring groups had taken place at these locations in previous occasions. Likely, black howlers store information of past social events at specific sites and recall such information to plan future travels. Memorising specific strategic locations where intergroup encounters have taken place provides defensibility advantages against the incursions of neighbouring groups. Different species of howler monkeys have been described to navigate towards neighbouring groups that emitted loud calls in proximity (*Alouatta guariba*, Cunha & Jalles-Filho, 2007; *Alouatta*

palliata, Hopkins, 2013; *Alouatta pigra*, Van Belle & Estrada, 2019). Hence, anticipating the location where potential intergroup encounters will take place enables howlers to plan their travel trajectory and approach neighbouring calls in a faster and potentially straighter manner. However, intergroup encounters in black howlers at PNP primarily happened at the borders of home ranges (Van Belle et al., 2013a; Van Belle et al., 2014). One could argue that increased turning at intergroup encounter locations might be a consequence of reaching the border of their home range instead of goal-directed behaviour (Nickaeen et al., 2017). Such a scenario is unlikely since there was no effect of home range overlap among study groups in the probability of approaching specific sites to howl in a goal-directed manner. Primates typically use a set of landmarks and the geometry of the landscape to create a frame of reference for spatial decision-making processes (Garber, 1998; Dolins, 2009; Cheng, 2010; Presotto & Izar, 2010; Hribar et al., 2011; Dolins et al., 2014). Home range boundaries are potentially established using such spatial cues in natural habitats and incorporated into the planning abilities of primates (Garber & Dolins, 2010).

I found that black howlers typically approached locations where loud calls had taken place previously in a goal-directed manner. In fact, approximately 84.4% of all recorded loud calling bouts occurred at locations where at least another loud calling bout was already recorded. While exploratory, this result suggests potential benefits from emitting loud calls at specific locations. First, the propagation of sound waves may reach further distances due to potentially obstruction-free locations, emergent trees or flat terrain areas (Ellinger & Hödl, 2012; Larsen & Radford, 2018). However, recent research found that black and gold howler monkeys' vocalisations did not differ in duration, frequency nor amplitude across an open-to-close vegetation gradient (Holzmann & Areta, 2020). Hence, howlers might be able to communicate across

habitats without being pressured to adjust the emission of their loud callings. An alternative explanation would be that, by consistently using specific locations to engage in loud calling bouts, black howlers are continuously updating neighbouring groups about the boundaries of their home range. Even though individuals and groups typically inform conspecifics about their identity through specific signals in their vocalizations (Yorzinski, 2017), environmental noise can influence the transmission of information. Thus, engaging in loud calling at locations that are recognisable by neighbouring groups might reinforce information regarding the identity of the group, which might be crucial to maintain their home range and avoid incursions from neighbouring groups (Feng et al., 2014).

Findings on route planning involving ecological events extend the growing body of evidence reported in other primate species (*Microcebus murinus*, Joly & Zimmerman, 2011; *Alouatta palliata*, Hopkins 2016; *Papio ursinus*, Noser & Byrne, 2007b; 2014; *Hylobates lar*, Asensio et al. 2011; *Pan troglodytes*, Ban et al., 2014; 2016). Black howler monkeys approached feeding sites in a goal-directed manner more often when fruits were present rather than young leaves or mature leaves. Due to the ephemeral and energy-rich nature of fruits, anticipating ripening periods and planning routes accordingly is highly valuable for animals in rainforests (Janmaat et al., 2016). Black howlers likely acquire knowledge regarding the productivity of fruit trees during previous experiences and used it to plan future routes to reach fruiting trees that otherwise would not have been detected either visually or olfactory. Indeed, Hopkins (2016) showed that mantled howlers travelled further distance to reach the largest fruit yields at a specific point in time. Similarly, other primate species both in the wild and captivity have been shown to anticipate the production, expiration and renewal rates of

different food types (Martín-Ordas et al., 2010; Haun et al., 2011; Rosati & Hare, 2012; Allen & Fortin, 2013; Templer & Hampton, 2013; Ban et al., 2014).

I found that black howlers appear to have evolved a strategy to cognitively cope with the spatiotemporal complexity of food resources. First, by selecting a subset of preferred feeding trees to memorize within their home range, the number of spatial elements to include into the cognitive process reduces. Similarly, Ban et al., (2016) showed that female chimpanzees selected a subset of rare feeding trees to remember likely due to their high content on fatty acids and carbohydrates in comparison to other trees. The enhanced nutritional and strategic importance of keystone trees for animals in rainforests has been widely documented in the literature for decades (Terborgh, 1986; Peres, 2000; Bleher et al., 2003; Watson & Herring, 2012; Milton et al., 2019). Filtering environmental information to focus the cognitive effort on memorising the location and phenological patterns of such valuable trees could be highly advantageous for primates in rainforests.

Second, by selecting preferred feeding trees with high phenological synchrony to memorise, the complexity of the cognitive process experienced an additional reduction. Since the probability of finding fruits in different individual trees from the same species varies dramatically in rainforests across tree species. selecting synchronous species will reduce the number of temporal elements to remember from the individual level to the species level. Hence, following a tree synchrony strategy to forage in rainforests might be more common than previously thought across primates (found in *Macaca fuscata*, Menzel, 1991; *Lophocebus albigena*, Janmaat et al., 2012; *Pan troglodytes*, Janmaat et al., 2013).

Primates benefit from the high levels of easily digestible sugar from fruits but also need the protein-rich content of young leaves to balance their diets (Lambert & Rothman, 2015). Trichromatic colour vision in howler monkeys has been suggested to be an adaptation that favours not only the detection of fruits but also young leaves by highlighting reddish colours against the background foliage (Melin et al., 2017). Contrary, I found no evidence that black howlers either planned routes to feed on young leaves nor selected a subset of trees with reduced spatiotemporal complexity to remember (as was found for fruits). My findings are in line with previous research on mantled howlers, where animals directed their long-distance travel bouts towards trees bearing fruit in the most palatable state while trees with new leaf flush were ignored (Hopkins, 2016).

The availability of young leaves is often described as about one order of magnitude higher than that fruit availability (Camaratta et al., 2016). Hence, young leaves are likely a less limiting factor than fruits (Milton, 1981). In addition, young leaf production typically increases during periods of maximum light radiation in tropical rainforests when water is available while fruit production is highly variant (Wright & Van Schaik, 1994; Lambert & Rothman, 2015). Both factors contribute to reduce the uncertainty of finding young leaves in rainforests, which potentially prevents the emergence of spatial memory associated with young leaf consumption (Riotte-Lambert & Matthiopoulus, 2019). However, the high variability of nutrient content – not only among trees of the same species but even within the same tree – highlights the importance of future fine-scale analyses incorporating nutritional analyses at individual tree level (Ganzhorn, 1992; Chapman et al., 2003; Ban et al., 2016).

The importance of these finding can be translated to the validation of inferring movement intentionality from ranging patterns combined with behavioural

observations. Although directional changes had been used to infer intentionality from large-scale ranging animals (Ban et al., 2014; 2016), here I validated the application of the CPT to infer cognitive skills in small–scale conditions. Yet, there is a remarkable importance of consistent and prolonged data collection periods to detect enough directional changes for statistical analyses in small–scale ranging species. For instance, baboons engaged in approximately five times more significant directional changes per day of observation than black howlers (baboons = 5.79 ± SD 1.99; black howlers = 1.07 ± SD 0.35), potentially as a consequence of the overall further distances travelled per day (baboons = 9.557 ± SD 487 m; black howlers = 366 ± SD 199 m; values from Noser & Byrne, 2014). In addition, even though Byrne's CPT will detect goal-directed behaviour from the study subjects (Byrne et al., 2009), it will never reflect all goal-directed behaviour. Goals can be located in a straight line or may not deviate enough from the previous location to be detected as a significant directional change. Hence, it is crucial to gather enough tracking data to avoid false negative results, which can mislead our understanding of animal spatial cognition.

According to my proposed hypotheses (Table 6.2), black howlers do not show as sophisticated cognitive skills to cope with the spatiotemporal complexity of their habitat as would be expected in other species. For instance, chimpanzees were described to continuously update their knowledge on local food sources in time and space and the species-specific differences of these levels, as well as the fruiting histories of individual trees (Janmaat et al., 2013; Ban et al., 2014; 2016; Janmaat et al., 2016). Further research should be considered to fill the blanks in the proposed set of hypotheses. First, I propose examining goal-directed behaviour towards feeding sites in other species of the genus *Alouatta*. While Mesoamerican howlers (e.g., *Alouatta pigra*) ingest a balanced leaf to fruit diet, Amazonian (e.g., *Alouatta belzebul*) and Atlantic (e.g.,

Alouatta guariba) species differ in that their diets are fruit and leaf-enriched respectively (Righini, 2014; Garber et al., 2015). The importance of generating memories associated with fruit consumption might differ across species depending on the relative importance fruits in the nutritional balance of the species (Asensio et al., 2011). Second, I suggest exploring goal-directed behaviour of primate species with similar socioecological traits but different brain to body size ratios: for example, ring-tailed lemurs (*Lemur catta*) and Western lowland gorillas (*Gorilla gorilla gorilla*). Although these species are group-living, highly cohesive and facultative-folivores primates (Watts, 1998; Sauther et al., 1999; Rogers et al., 2004), there is a clear divergence in brain size relative to body size that might conditioned their cognitive skills (Deaner et al., 2014; Rosati, 2017). Finally, incorporating both solitary primate species (e.g., *Pongo pygmaeus*) and species with complex societies (e.g., *Ateles geoffroyii*) that include a high proportion of fruits in their diets will shed light on the potential bias towards social stimuli in the generation of episodic memories. Overall, the present framework provides a tool for future comparative studies that can shed light on the ontogeny and evolution of non-human primate spatial cognition.

Chapter 7: General Discussion

7.1 Summary

Ever since Carpenter's (1934) pioneering work describing travelling behaviour in mantled howlers, we have expanded our knowledge not only in spatial skills and movement patterns of howler monkeys but also in various other non-human primate species (Trapanese et al., 2018; Tujague & Janson, 2018). Yet, documented inconsistencies and the lack of long-term, detailed datasets on most howler species' movement ecology have highlighted the importance of an in-depth study (Fortes et al., 2015). We conducted the most comprehensive navigation study in a Neotropical primate to date (Tujague & Janson, 2018) with the aim of understanding black howlers' foraging cognition. Throughout this research, I addressed different aspects related to the foraging cognition of the species, from its ability to code structural spatial information to memories, and the benefits associated with their described navigation strategy. Overall, I provide a detailed overview of black howlers' spatial skills combining different analytical techniques, which have replicability potential in future studies.

In agreement with studies on mantled howler monkeys (Milton 1981; Hopkins, 2011; 2013), the primary navigation strategy reported by black howlers at PNP was a route based cognitive map. Black howlers' route network extended throughout their entire home range and was used to systematically revisit main feeding sources. Similarly, I found a high number of nodes connecting habitual route segments, which likely optimised howlers' movement decision making to reach specific goals.

Subsequently, I described the benefits associated with route navigation in a heterogeneous landscape. Black howlers located their habitual route segments in areas that enhanced the visual access to potential food sources while travelling. Howlers are likely prioritising monitoring potential food resources while travelling with the effect of reducing their cognitive load and enhancing the process of movement decision-making. In addition, black howlers avoided locating habitual routes in areas nearby canopy gaps. Highly used route segments were located in elevated areas within black howlers' home ranges but only when food sources were not visible. Therefore, route navigation was shown to provide cognitive and energetic benefits to black howlers despite potentially constraining their movement flexibility.

Contrary to my predictions, I did not find evidence suggesting that black howlers were able to optimise the trajectory of their movement patterns under conditions of varying food availability, experience or intragroup competition. According to our results, the main factor dictating the linearity of black howlers' trajectories was the shape of their route network. Such strong reliance on route navigation likely increased the energy spent on travelling and suggests that black howlers are not able to engage in cognitively flexible movement patterns. In addition, fission-fusion primate species showed overall higher linearity values than primate species that travel cohesively – or solitarily – suggesting the importance of route navigation on promoting coordinating movement in groups.

Finally, black howlers showed evidence of goal-directed behaviour towards locations where relevant social and ecological events had taken place previously. The monkeys intentionally returned to locations where intergroup encounters had taken place previously with the goal of engaging in loud calling bouts. Similarly, goal-directed behaviour was shown towards feeding trees that contained fruit at that specific

moment in time with the goal of feeding on these trees again. Specifically, the monkeys exhibited goal-directed behaviour by feeding on fruits of targeted preferred trees that presented synchronous phenological cycles, suggesting that howlers prioritise memorising few spatial locations with simple temporal cycles. Goal-directed behaviour towards such sites is interpreted here as a potential candidate for planning skills and, thus, episodic-like memory.

The combination of these results provide evidence to suggest that black howlers do not exhibit flexible spatial skills, yet they are able to engage in advantageous navigation patterns by constructing efficient route networks throughout their home ranges. The overall structure and location of these route networks was proven to facilitate travelling decisions while promoting resource monitoring and energy saving. In addition, black howlers' limited spatial flexibility might be compensated by cognitive mechanisms that promote memories associated with specific locations and contexts. Such a trade-off between cognitive flexibility and memory was likely favoured by the stability of the environment in which black howlers live (Tello-Ramos et al., 2019).

7.2 Theoretical framework

7.2.1 Cognitive implications

Spatial cognition has been a pivotal element in the study of developmental and comparative psychology, evolutionary anthropology and, more recently, movement ecology (Shettleworth, 2010; Milton, 1981; Dunbar & Shultz, 2007; Nathan et al., 2008). Advances in understanding animal and human spatial skills during the last decades focused on cognitive laboratories in the absence of realistic socioecological variables (Janmaat, 2019). Since cognition evolved as an adaptation of individuals to their living conditions, cognitive lab studies need to be contrasted with the behaviour of individuals in their natural habitats to be validated (Jacobs & Menzel, 2014; Boesch, 2020).

Studying cognition in the wild can help advance the theoretical framework of cognition and avoid the oversimplification of cognitive processes (Wittig & Crockford, 2018; Janmaat, 2019). For instance, the dichotomy that characterizes the study of animal cognitive maps (i.e., route based versus coordinate based cognitive maps) finds its roots in experiments in rats testing their capacity to engage in short-cuts when moving in mazes (Tolman, 1948; Menzel, 1973; Cheng, 1986). Subsequent studies in captive settings and wild populations developed their theoretical hypotheses from these baselines (Poucet, 1993; Garber, 2000; Normand & Boesch, 2009; de Raad & Hill, 2019). However, current cognitive research has revealed that animal cognition and behaviour are more plastic than previously thought, highlighting the importance of considering traits as a continuum instead of unique features (Morand-Ferron, 2017; Aureli & Schino, 2019; Warren, 2019). Here, after describing general traits associated with cognitive maps, I examined navigation flexibility as a gradient assessing black howlers' abilities to optimise their travel trajectories using linearity as a proxy. Results

consistently supported the hypothesis that black howlers strongly rely on routes to navigate and do not engage in flexible movement patterns. Such consistency in results is not typically found in the literature, where contradictory findings have been explained as the co-existence of both cognitive maps in the same population, which are used under different conditions (Presotto & Izar, 2010; Porter & Garber, 2013; Presotto et al., 2019). Moving from a combinatory approach in which spatial skills are assessed as a species' ability to switch between two behavioural states towards a multimodal approach that expresses species spatial flexibility as a continuum – or gradient – will likely provide a more accurate framework for future comparative studies (Warren, 2019). Bertolani (2013) even advocates for erasing the concept of the Euclidean map in future research due to its consistent lack of support across studies in different taxa. Indeed, adjusting our approach in the examination of spatial cognition will bring up nuances to better understand animal cognitive evolution.

Even though exploring differences in navigation flexibility among individuals and groups will be a step forward, it needs to be assessed in combination with memory. Tello-Ramos et al., (2019) provided an extensive review highlighting an adaptive trade-off between both cognitive processes (i.e., spatial flexibility versus memory), which varied as a function of the stability of the landscape wherein individuals live. The authors suggest that this trade-off is mediated by the energetic costs of cognitive processes (Tello-Ramos et al., 2019). Maintaining synaptic connections over prolonged periods of time (i.e., memory; Plaçais & Preat, 2013) requires similar energetic supplies than continuously generating short-term, new synapses (i.e., spatial flexibility; Mery & Kawecki, 2003), which suggests that animal species can only energetically support one of these processes (e.g., migratory mule deer, *Odocoileus hemionus*, Sawyer et al., 2018; Augusto-Oliveira et al., 2019). If an individual or group inhabits a rapidly

changing landscape, the value of remembering previously learnt information will decrease while the ability of learning new associations should be favoured (Riotte-Lambert & Matthiopoulos, 2020). Moreover, memory retention will be highly beneficial in stable and predictable landscapes (Riotte-Lambert & Matthiopoulos, 2020). In Chapter 6, I provide strong evidence of goal-directed behaviour in black howlers, which is likely representative for planning skills and episodic-like memory (Asensio et al., 2011). Generating memories is probably more advantageous for black howlers at PNP than constantly renewing the environmental information stored in their neural system. PNP showed relatively stable intra-annual NDVI values with a sharp increase after the rainy season. However, a correct estimation of PNP's ecological stability would require developing a model of environmental predictability based on larger temporal scales (i.e., multiannual NDVI cycles, Peters et al., 2017). Overall, results presented in this thesis potentially agree with the cognitive trade-off presented by Tello-Ramos et al., (2019) but further assessments of landscape predictability are needed to be carried out.

In addition, both navigation flexibility and spatial memory are independently structured by a series of domain-specific cognitive modules nested within each cognitive process but also by transversal general cognitive modules (Burkart et al., 2017). While the former modules can only be applied to solve problems for which they evolved (e.g., spatial memory to retrieve stored food in scatter-hoarder animals, Delgado & Jacobs, 2017), the latter can be used to solve problems across domains (Burkart et al., 2017). For instance, if an individual is able to engage in flexible behavioural patterns in social interactions and navigation, cognitive flexibility is likely a transversal cognitive module. The more transversal or general a cognitive module is, the more energy it will demand to be maintained. Therefore, examining universality of cognitive processes across domains or contexts will be indicative of the relative

influence of cognitive modules on the overall cognitive capacity of the animal (Fig. 7.1; Burkart et al., 2017). Each animal species is characterized by an overall cognitive capacity, which determines the amount of information that can be processed at a given moment (i.e., cognitive load; see also Milton, 2000). According to our results, black howlers showed a series of strategies to minimize the amount of information to process

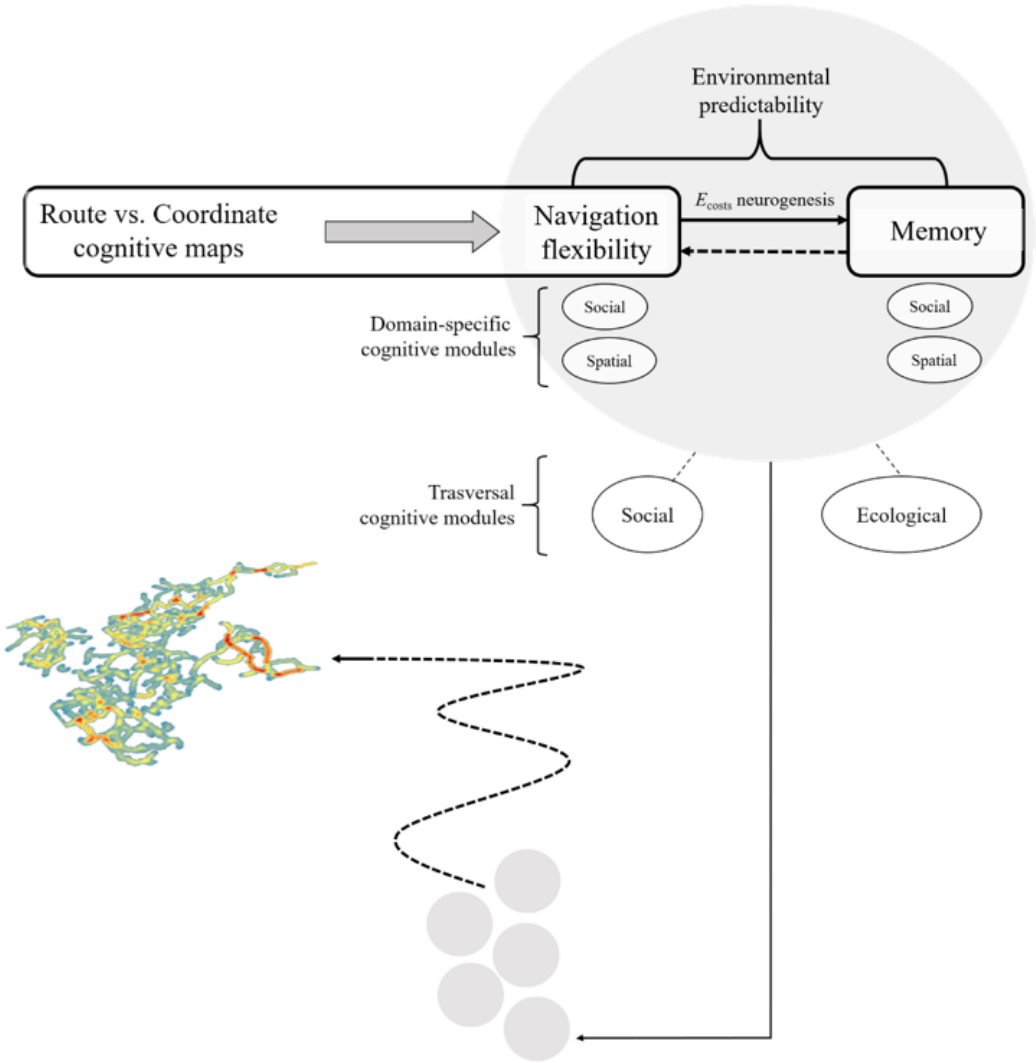


Figure 7. 1 Graphic summary of the results framed into current cognitive theories. The general cognitive state of an individual (big, grey sphere) emerges as the trade-off between cognitive flexibility and memory, and contributes for the group's "intelligence" (small, grey spheres) to generate efficient route networks through time.

during movement decisions as monitoring feeding trees and memorising phenological patterns of preferred, highly synchronous fruit trees only. It is likely that group living animals overcome potential limitations imposed by individual's spatial cognitive load by relying on: 1) the information gathered by conspecifics through their own personal experience (Delgado et al., 2018); and, 2) the information accumulated within the group through generations (Biro et al., 2016; Sasaki & Biro, 2017). I argue that, by living in groups, black howlers potentially optimise their route networks over time by incorporating information gathered by different individuals, which is likely transmitted intergenerationally via social learning while travelling. In addition, the sporadic incorporation of novel individuals through dispersal would bring in novel environmental information. As a result, black howlers develop an efficient route network in terms of connectivity and landscape interactions and overcome potential limitations of their cognitive load (Fig. 7.1).

7.2.1 Evolutionary implications

Over the course of human evolution, there have been a series of steps in which a reconfiguration in spatial cognition was crucial for the survival of our predecessors. The emergence of new spatially and temporally unpredictable food sources such as fruits, the transition from a three-dimensional scenario in the canopy to ground-based movement and the role of language in sharing spatially-explicit information are paradigms narrowly linked with human and non-human primate evolution (Haun et al., 2006; Corballis, 2019). Our findings can provide insights into these evolutionary questions and help to understand the current primate cognitive status.

Early primate diversification occurred around 70 million years ago (78 – 64 million years ago, Steiper & Seiffert, 2012), a period in which the angiosperms (i.e., monophyletic group of plants that contain all species that produce flowers and fruits) increased from 0 to 80 % (Meredith et al., 2011). Gómez & Verdú, (2012) summarized a series of phylogenetic and paleontological evidence that highlight the coevolution of angiosperms and primates in a mutualistic scenario. While angiosperms would benefit from primates, which would act as pollinators and seed dispersers, primates would benefit from the energy-rich content of fruits (Sussman et al., 2013). Thus, the cognitive pressure of locating fruits across rainforests arose in primates alongside their coevolution with angiosperms (Milton, 1981). These small bodied, ancient proto-primates likely engaged in conservative movements that increased the likelihood of encountering fruit trees (i.e., returning to already visited fruit trees through the same tree sequence, Milton, 1981). By repeatedly travelling through the same tree sequences where fruit had already been found, seeds from those same fruit species would have been dispersed along the way increasing the likelihood of finding the same fruit species over time (Di Fiore & Suarez, 2007). Alternatively, other primate lineages would have evolved more sophisticated cognitive skills favouring flexible navigation (Milton, 1981). Hence, primate diversification in navigation strategies was likely parallel to the diversification of angiosperms and primate radiation.

The transition from arboreality to terrestriality in early humans occurred between 6 – 4.4 million years ago (Lovejoy, 2009). It progressively led to bidepdalism, which triggered a series of morpho-anatomical adaptations among early humans characterized by a continuous expansion of brain size for the next 3 million years (Rosenberg & Trevathan, 1995; Seymour et al., 2016). In addition to increasing in size, the brains of early humans experienced an anatomical reconfiguration during this time

(Barton & Harvey, 2000), which might have been translated into a cognitive reconfiguration as well. In terms of spatial cognition, transferring from a three-dimensional space in the canopy to ground-based movements changes the importance of coding information on the vertical axis (Burt de Perera et al., 2016). In addition, open habitats, such as savannahs, have been identified as the most parsimonious scenario for the emergence of bipedalism (Reed, 1997), where the acquisition of information on the horizontal axis might have been prioritised (e.g., to avoid predators, Isbell et al., 2018). Progressively, early hominins extended their daily range across savannahs as a response to the diminished availability of food resources (Isbell & Young, 1996). It is likely that individuals that were able to integrate spatial information over large-scales and enhance their navigational skills would gain more access to food resources and ultimately enhance their fitness compared to cognitively constrained individuals (Vashro & Cashdan, 2014). Therefore, bipedalism involved a cognitive reconfiguration of space triggered by a prevalence of the horizontal axis in combination with an increment in the cognitive load required for efficient navigation.

Similarly, the emergence of human language, between 500,000 – 300,000 years ago, has been described as a key step in the evolution of spatial cognition (Wildgen, 2004). Oleksiak et al., (2011) revealed that although humans present a strong cerebral lateralization in which spatial information is primarily processed in the right hemisphere, monkeys process spatial information in both the left and the right hemisphere. Human language is supported by the left brain hemisphere, which suggests that the emergence of language competence in the left hemisphere triggered human brain lateralization (Corballis, 2019). Haun et al., (2006) showed that non-verbal children and great apes engaged in similar spatial cognitive strategies by which they remembered places in space instead of spatial associations while verbal children

managed to generate spatial associations. Further, spatial associations between physical objects or locations are coded differently across languages modifying the perception of space among cultures (Majid et al., 2004). For instance, while Namibian elementary school children (Hai||om language) processed spatial releationships using an absolute frame of reference (i.e., North-South), Dutch children used a relative frame of reference (i.e., right-left; Haun et al., 2011). Haun et al., (2011) described that each dominant linguistic strategy consistently correlated with preferred cognitive strategies across a series of tasks and restrained children to switch their frame of reference on demand. In line with this, chimpanzees have been shown to use a wide range of vocalizations (Schel et al., 2013), gestures (Hobaiter & Byrne, 2014) and a combination of both (Hobaiter et al., 2017) to intentionally transfer specific information to conspecifics. While the complexity of human language outranges chimpanzee's communication skills, the underlying cognitive process that support such advance transfer of information among chimpanzees may support their sophisticated spatial skills. Therefore, the emergence of language has been proposed to support but also to condition the spatial skills across humans. However, the relationship between non-human primates' communication skills and their ability to code spatial relationships still needs to be explored and can help to understand the evolution of navigational strategies.

7.3 Methodological implications

Studies of foraging cognition in the wild face several analytical challenges, including avoiding circular arguments (Hahn, 2011), controlling for spatial autocorrelation (Cushman, 2010), the importance of scale in movement and landscape analyses (Mann et al., 2014) and the absence of null models and controls in statistical analyses (Janmaat, 2019). In this thesis, I developed, applied and validated a series of analytical tools which overcame several of these obstacles, and that can be used in future research on foraging cognition. This is especially important since the conditions of every study population vary widely; therefore, having a wider and more rigorous set of tools available will enable researchers to select the most appropriate analyses to answer specific cognitive research questions.

I inferred the influence of landscape heterogeneity in the movement patterns of black howlers by developing a "visibility index". This index avoided circular reasoning by including the locations of all potential feeding trees instead of only including feeding trees in which howlers were observed feeding (Chapter 4). Subsequently, I avoided spatial autocorrelation issues by incorporating a term in the model that controlled for spatial correlation among residuals (see Fürtbauer et al., 2011 for details). Similarly, I developed a framework to test the influence of resources' spatiotemporal complexity into black howlers' planning skills (Chapter 6). By incorporating howlers' preferences towards specific feeding sites and phenological synchronicity as predictor variables, I could determine which level of spatiotemporal complexity black howlers can remember. Under similar data collection protocols, both methods can be applied to future studies on wild animal spatial cognition.

I applied, for the first time, existing network analyses to describe navigation efficiency in wild primates' route networks (Chapter 3). In addition, I validated the method by running random movement simulations to generate a random set of route networks and comparing both models (Chapter 3). Simulating movements on such small-scale has rarely been done and can be an important step towards using "movement controls" against which to test future hypotheses related with foraging cognition (Suarez et al., 2014). Similarly, I validated methods commonly used to analyse large scale ranging patterns for small scale ranging primates, such as remote sensing imagery to estimate vegetation activity (Chapter 5) and to the detection of significant directional changes in movement trajectories (i.e., CPT; Chapter 6).

7.4 Movement and conservation

The relationship between movement ecology and conservation may not be obvious at first glance but there are relevant advantages from building bridges between both fields (Allen & Singh, 2016; Westley et al., 2018; but see Caro, 2007 for a critical approach). I propose three specific scenarios in which the analyses presented in this thesis could be applied into conservation programs but also how the same analyses could be optimised through conservation measures (Fig. 7.2).

Firstly, tracking wild populations in order to describe their route network will help identifying highly used route segments and nodes. Intersecting newly created wildlife corridors with such nodes, which are locations where environmental information is increasingly perceived, will likely enhance the flow of animals among isolated areas (LaPoint et al., 2013). In turn, newly created wildlife corridors can help determine animals' ability to engage in short-cuts in order to reach new goals. Secondly, examining the characteristics of route networks in relationship to landscape attributes and food resources will promote the selection of suitable areas to translocate groups

(Kemink & Kesler, 2013; Poindexter, 2017). Upon translocation, it will be possible to examine the ability of "naïve" groups to generate and optimise their route network in real time. Thus, the value of socially transmitted navigation information can be elucidated together with the potential emergence of pro-cultural traits related with navigation (Spiegel & Crofoot, 2016; Berdahl et al., 2018). Finally, the formulation of population models to predict demographic fluctuations will be enhanced by estimating a species fruit foraging effort based on their cognitive skills instead of only focusing on the availability of food sources (Dukas, 2004). Most animal species will not forage on as many food resources as they can but will reuse the ones they remember and anticipate their temporal patterns (Dukas, 2004). Therefore, estimating resource intake through resource availability alone may not be optimal. Such population models will provide information on the value of spatial skills in terms of population fitness, which likely differs among both species and populations in habitats with different spatiotemporal patterns of resource availability.

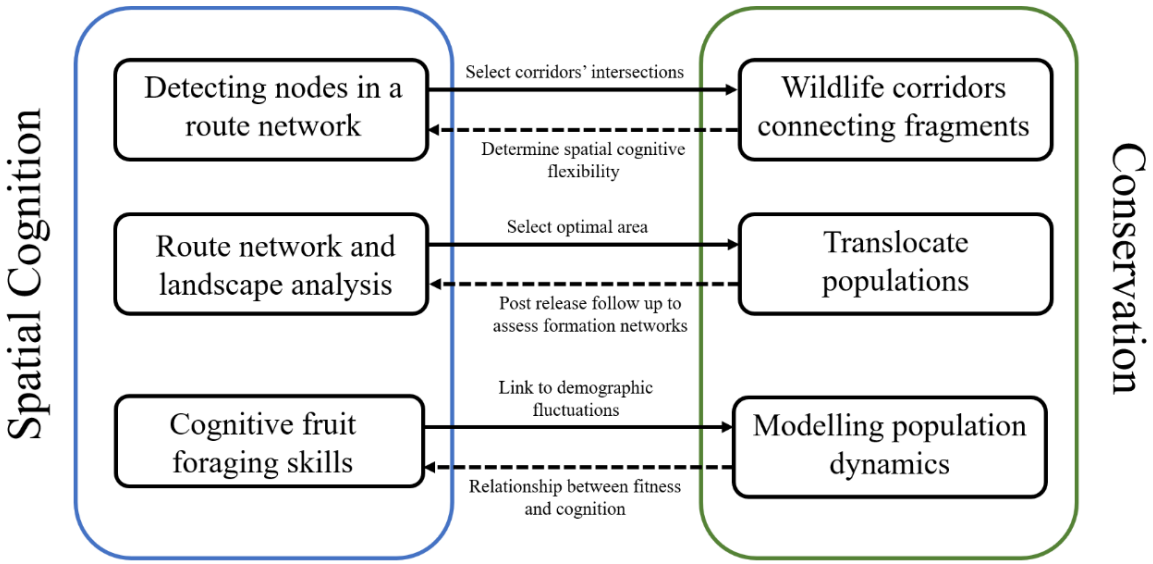


Figure 7. 2 Potential applications of patterns described in spatial cognition studies into conservation measures and *vice versa*.

7.5 Future lines of research

The current technological scenario provides opportunities for gathering large quantities of tracking data, while advanced analytical tools allow inferring patterns associated with the cognition of animals in a wide variety of contexts. For example, Meekan et al., (2017) highlights the power of algorithms used to estimate human mobility relying on the use of massive datasets, which account for hundreds of individuals moving across ecosystems. Such algorithms have not only provided insights into processes such as the spread of emergent infectious diseases (e.g. Ebola virus in bats, Leroy et al., 2009), but have also enabled researchers to monitor the propagation of ideas, opinions and innovations within human societies (Mocanu et al., 2013). As the amount of tracking data collected for animal studies is increasing on an annual basis, the likelihood of applying such algorithms into animal movement increases (Kays et al., 2015; Thums et al., 2018). Here, I propose three potential lines of future research based on current and proximate technological scenarios to move forward the field of foraging cognition:

(1) The development of universal methods to infer cognition across populations and species in the wild. While most studies focus on tailoring the analyses of spatial cognition to the study species, the extensive collection on primate ranging data worldwide provides a real opportunity to compare cognition across species and populations (Reyna-Hurtado et al., 2018; Jang et al., 2019b). With collaborators, I have started a project with the objective of selecting a series of response variables (e.g., travelling linearity between goals, time lapse between revisiting events, sequential order of visitations) using predictor variables such as experience (i.e., familiarity) or environmental predictability (i.e., variability of food sources in time

and space) in statistical models that would control for cofounding variables (e.g., habitat type) and phylogeny.

(2) The systematisation of the study of route networks in wild populations. Network analyses can provide useful information regarding the efficiency and complexity of wild primate movement patterns. Applying the body of analyses developed in urban transport networks into the static route networks of wild primates is a new and promising line of research. Firstly, applying the HRAM (Habitual Route Assessment Method, Presotto et al., 2019, Supplementary Material) can systematise the description of habitual routes from tracking data and minimize manual work. Secondly, since it is not possible to compare two networks in different locations due to spatial cofounding factors, it would be necessary to generate a random route network as presented in Chapter 3. Then, we would compare the structure of observed and simulated route networks by calculating the overall "dissimilarity distance" (i.e., how similar these networks are between them, Schieber et al., 2017) as an index. Such index can be used to compare differences between simulated and observed route networks across populations and species (Schieber et al., 2017).

(3) To introduce virtual reality as a tool for cognitive comparative studies among captive and wild populations. Presenting nonhuman primates virtual simulated environments provides an ideal opportunity to gain insights into their navigational strategies and spatial abilities (Naik et al., 2020). The navigational strategies shown by naïve, captive individuals that had never been in touch with their natural habitat with naturalistic observations in the wild can provide meaningful insights into the cognitive plasticity of species (Janmaat, 2019). For instance, by testing different species under the same virtual scenario, in which environmental conditions can be controlled, valuable insights into inter-species cognitive abilities can be elucidated

(Dolins et al., 2017). Creating a trade-off between ecological validity and experimental control in future collaborations among naturalistic and captive research on foraging cognition is a promising pathway that will advance the field of comparative psychology.

Bibliography

Agostini, I., Holzmann, I., & Di Bitetti, M. S. (2010). Ranging patterns of two syntopic howler monkey species (*Alouatta guariba* and *A. caraya*) in Northeastern Argentina. *International Journal of Primatology*, 31(3), 363–381. DOI:10.1007/s10764-010-9390-x

Allen, A. M., & Singh, N. J. (2016). Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution*, 3, 155. DOI:10.3389/fevo.2015.00155

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49(3/4), 227–267.

Altmann, S. A., & Altmann, J. (1977). On the analysis of rates of behaviour. *Animal Behaviour*, 25(2), 364–372. DOI:10.1016/0003-3472(77)90011-2

Amato, K. R. (2019). Missing Links: the role of primates in understanding the human microbiome. *Msystems*, 4(3), e00165-19. DOI:10.1128/mSystems.00165-19

Amato, K. R., & Garber, P. A. (2014). Nutrition and foraging strategies of the black howler monkey (*Alouatta pigra*) in Palenque National Park, Mexico. *American Journal of Primatology*, 76(8), 774–787. DOI:10.1002/ajp.22268

Amato, K. R., & Righini, N. (2015). The howler monkey as a model for exploring host-gut microbiota interactions in primates. In M.M. Kowalewski, P. A. Garber, L. Cortes-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behavior, ecology, and conservation* (pp. 229–258). DOI:10.1007/978-1-4939-1957-4_9

Amato, K. R., Van Belle, S., & Wilkinson, B. (2013). A comparison of scan and focal sampling for the description of wild primate activity, diet and intragroup spatial relationships. *Folia Primatologica*, 84(2), 87–101. DOI:10.1159/000348305

Amici, F., Barney, B., Johnson, V. E., Call, J., & Aureli, F. (2012). A modular mind? A test using individual data from seven primate species. *PLoS ONE*, 7(12), e51918. DOI:10.1371/journal.pone.0051918

Amici, F., Call, J., Watzek, J., Brosnan, S., & Aureli, F. (2018). Social inhibition and behavioural flexibility when the context changes: A comparison across six primate species. *Scientific Reports*, 8(1), 1–9. DOI:10.1038/s41598-018-21496-6

Ancrenaz, M., Sollmann, R., Meijaard, E., Hearn, A. J., Ross, J., Samejima, H., … Wilting, A. (2015). Coming down from the trees: is terrestrial activity in Bornean orangutans natural or disturbance driven? *Scientific Reports*, 21(5), 487–499. DOI:10.1038/srep04024

Angilletta, M. J., Roth, T. C., Wilson, R. S., Niehaus, A. C., & Ribeiro, P. L. (2008). The fast and the fractalous: speed and tortuosity trade off in running ants. *Functional Ecology*, 22(1), 78–83. DOI:10.2307/20142775

Aristide, L., Dos Reis, S. F., Machado, A. C., Lima, I., Lopes, R. T., & Ivan Perez, S. (2016). Brain shape convergence in the adaptive radiation of New World monkeys.

Proceedings of the National Academy of Sciences, 113(8), 2158–2163. DOI:10.1073/pnas.1514473113

Arroyo-Rodríguez, V., & Dias, P. A. D. (2010). Effects of habitat fragmentation and disturbance on howler monkeys: a review. *American Journal of Primatology*, 72(1), 1–16. DOI:10.1002/ajp.20753

Asensio, N., Brockelman, W. Y., Malaivijitnond, S., & Reichard, U. H. (2011). Gibbon travel paths are goal oriented. *Animal Cognition*, 14(3), 395–405. DOI:10.1007/s10071-010-0374-1

Augusto-Oliveira, M., Arrifano, G., Malva, J., & Crespo-Lopez, M. (2019). Adult hippocampal neurogenesis in different taxonomic groups: possible functional similarities and striking controversies. *Cells*, 8(2), 125. DOI:10.3390/cells8020125

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., … Van Schaik, C. P. (2008). Fission-fusion dynamics new research frameworks. *Current Anthropology*, 49(4), 627–654. DOI:10.1086/586708

Aureli, F., & Schino, G. (2019). Social complexity from within: how individuals experience the structure and organization of their groups. *Behavioral Ecology and Sociobiology*, 73(1), 1–6. DOI:10.1007/s00265-018-2604-5

Avgar, T., Baker, J. A., Brown, G. S., Hagens, J. S., Kittle, A. M., Mallon, E. E., … Fryxell, J. M. (2015). Space-use behaviour of woodland caribou based on a cognitive movement model. *Journal of Animal Ecology*, 84(4), 1059–1070. DOI:10.1111/1365-2656.12357

Azevedo, F. A. C., Carvalho, L. R. B., Grinberg, L. T., Farfel, J. M., Ferretti, R. E. L., Leite, R. E. P., … Herculano-Houzel, S. (2009). Equal numbers of neuronal and nonneuronal cells make the human brain an isometrically scaled-up primate brain. *Journal of Comparative Neurology*, 513(5), 532–541. DOI:10.1002/cne.21974

Baddeley, B., Graham, P., Husbands, P., & Philippides, A. (2012). A model of ant route navigation driven by scene familiarity. *PLoS Computational Biology*, 8(1). DOI:10.1371/journal.pcbi.1002336

Balaban-Feld, J., Mitchell, W. A., Kotler, B. P., Vijayan, S., Tov Elem, L. T., Rosenzweig, M. L., & Abramsky, Z. (2019). Individual willingness to leave a safe refuge and the trade-off between food and safety: a test with social fish. *Proceedings of the Royal Society B: Biological Sciences*, 286(1907), 20190826. DOI:10.1098/rspb.2019.0826

Baltisberger, C., Laska, M., & Rodríguez-Luna, E. (2003). Olfactory communication in mantled howler monkeys (*Alouatta palliata*)—a field study. *Folia Primatologica*, 74, 183–184.

Ban, S. D., Boesch, C., & Janmaat, K. R. L. (2014). Taï chimpanzees anticipate revisiting high-valued fruit trees from further distances. *Animal Cognition*, 17(6), 1353–1364. DOI:10.1007/s10071-014-0771-y

Ban, S. D., Boesch, C., N'Guessan, A., N'Goran, E. K., Tako, A., & Janmaat, K. R. L. (2016). Taï chimpanzees change their travel direction for rare feeding trees providing fatty fruits. *Animal Behaviour*, 118, 135–147.

DOI:10.1016/j.anbehav.2016.05.014

Barelli, C., Boesch, C., Heistermann, M., & Reichard, U. H. (2008). Female white-handed gibbons (Hylobates lar) lead group movements and have priority of access to food resources. *Behaviour*, 145(7), 965–981.

Barks, S. K., Calhoun, M. E., Hopkins, W. D., Cranfield, M. R., Mudakikwa, A., Stoinski, T. S., … Sherwood, C. C. (2015). Brain organization of gorillas reflects species differences in ecology. *American Journal of Physical Anthropology*, 156(2), 252–262. DOI:10.1002/ajpa.22646

Barnhart, E. L. (2001). *The Palenque mapping project: settlement and urbanism at an ancient Maya city*. University of Texas at Austin.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: keep it maximal. *Journal of Memory and Language*, 68(3), 255–278. DOI:10.1016/j.jml.2012.11.001

Barrat, A., Barthélemy, M., & Vespignani, A. (2005). The effects of spatial constraints on the evolution of weighted complex networks. *Journal of Statistical Mechanics: Theory and Experiment*, 05, P05003. DOI:10.1088/1742-5468/2005/05/p05003

Barthélemy, M. (2011). Spatial networks. *Physics Reports*, 499(1–3), 1–101. DOI:10.1016/j.physrep.2010.11.002

Barton, R. A., & Harvey, P. H. (2000). Mosaic evolution of brain structure in mammals. *Nature*, 405(6790), 1055–1058. DOI:10.1038/35016580

Bast, H., Delling, D., Goldberg, A., Müller-Hannemann, M., Pajor, T., Sanders, P., … Werneck, R. F. (2016). Route planning in transportation networks. In L. Kliemann & P. Sanders (Eds.), *Algorithm engineering* (pp. 19–80). DOI:10.1007/978-3-319-49487-6

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. DOI:10.18637/jss.v067.i01

Bates, L. A., Poole, J. H., & Byrne, R. W. (2008). Elephant cognition. *Current Biology*, 18(13), R544–R547.

Bebko, A. O. (2018). *Ecological and cognitive influences on Orangutan space use*. York University.

Behie, A. M., & Pavelka, M. S. M. (2015). Fruit as a key factor in howler monkey population density: conservation implications. In M.M. Kowalewski, P. A. Garber, L. Cortes-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behavior, ecology, and conservation*. DOI:10.1007/978-1-4939-1960-4_13

Behrens, T. E. J., Muller, T. H., Whittington, J. C. R., Mark, S., Baram, A. B., Stachenfeld, K. L., & Kurth-Nelson, Z. (2018). What is a cognitive map? Organizing knowledge for flexible behavior. *Neuron*, 100(2), 490–509. DOI:10.1016/j.neuron.2018.10.002

Bell, W. J. (1991). *Searching behaviour: the behavioural ecology of finding resources*. London: Chapman & Hall.

Benhamou, S. (2004). How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology*, 229, 209–220. DOI:10.1016/j.jtbi.2004.03.016

Bennett, A. T. D. (1996). Do animals have cognitive maps? *The Journal of Experimental Biology*, 199, 219–224.

Berdahl, A. M., Kao, A. B., Biro, D., Flack, A., Westley, P. A. H., Codling, E. A., … Dell, A. I. (2018). Collective animal navigation and migratory culture: from theoretical models to empirical evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1746), 20170009. DOI:10.1098/rstb.2017.0009

Berg, H. C. (2000). Motile behavior of bacteria. *Physics Today*, 53(1), 24–29. DOI:10.1063/1.882934

Berger-Tal, O., & Bar-David, S. (2015). Recursive movement patterns: review and synthesis across species. *Ecosphere*, 6(9), art149. DOI:10.1890/ES15-00106.1

Bergeson, D. J. (1998). Patterns of suspensory feeding in *Alouatta palliata*, *Ateles geoffroyi*, and *Cebus capucinus*. In E. Strasser, J. G. Fleagle, A. L. Rosenberger, & H. M. McHenry (Eds.), *Primate locomotion* (pp. 45–60). DOI:10.1007/978-1-4899-0092-0_3

Bergman, C. M., Schaefer, J. A., & Luttich, S. N. (2000). Caribou movement as correlated random walk. *Oecologia*, 123, 364–374.

Bertolani, P. (2013). *Ranging and travelling patterns of wild chimpanzees at Kibale, Uganda:a GIS approach*. University of Cambridge.

Bicca-Marques, J. C., Chaves, Ó. M., & Hass, G. P. (n.d.). Howler monkey tolerance to habitat shrinking: lifetime warranty or death sentence? *American Journal of Primatology*, e23089. DOI:10.1002/ajp.23089

Biewener, A. (1990). Biomechanics of mammalian terrestrial locomotion. *Science*, 250(4984), 1097–1103. DOI:10.1126/science.2251499

Biewener, Andrew, & Patek, S. N. (2018). *Animal locomotion* (Andrew Biewener & S. N. Patek, Eds.). Oxford, UK: Oxford University Press.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, 6(4), 213–223. DOI:10.1007/s10071-003-0183-x

Biro, D., Sasaki, T., & Portugal, S. J. (2016). Bringing a time-depth perspective to collective animal behaviour. *Trends in Ecology and Evolution*, 31(7), 550–562.

Bivand, R., Keitt, T., & Rowlingson, B. (2018). *rgdal: Bindings for the "Geospatial" Data Abstraction Library*.

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, 48(3), 653–667. DOI:10.1006/anbe.1994.1285

Boesch, C. (2020). The human challenge in understanding animal cognition. In L. S. M. Johnson, A. Fenton, & A. Shriver (Eds.), *Neuroethics and nonhuman animals* (pp. 33–51). DOI:10.1007/978-3-030-31011-0_3

Boesch, C., & Boesch, H. (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, 13(5), 415–440. DOI:10.1016/S0047-2484(84)80055-X

Boinski, S., Treves, A., & Chapman, C. A. (2000). On the move: how and why animals travel. In S. Boinski & P. A. Garber (Eds.), *On the move: how and why animals travel* (pp. 43–72). Chicago, US: University of Chicago Press.

Boonratana, R. (2000). Ranging behavior of proboscis monkeys (*Nasalis larvatus*) in the Lower Kinabatangan, northern Borneo. *International Journal of Primatology*, 21(3), 497–518. DOI:10.1023/A:1005496004129

Bracis, C., Bildstein, K. L., & Mueller, T. (2018). Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography*, 41(11), 1801–1811. DOI:10.1111/ecog.03618

Bracis, C., & Mueller, T. (2017). Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proceedings of the Royal Society B: Biological Sciences*, 284(1855), 20170449. DOI:10.1098/rspb.2017.0449

Bridgeman, L. L. (2012). *The feeding ecology of Yucatán black howler monkeys (Alouatta pigra) in mangrove forest, Tabasco, Mexico* (Washington University in St. Louis). Washington University in St. Louis.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., … Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400. DOI:10.3929/ETHZ-B-000240890

Brower, L. (1996). Monarch butterfly orientation: missing pieces of a magnificent puzzle. *Journal of Experimental Biology*, 199(1).

Burgess, N. (2006). Spatial memory: how egocentric and allocentric combine. *Trends in Cognitive Sciences*, 10(12), 551–557. DOI:10.1016/j.tics.2006.10.005

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron*, 35(4), 625–641. DOI:10.1016/S0896-6273(02)00830-9

Burkart, J. M., Schubiger, M. N., & van Schaik, C. P. (2017). The evolution of general intelligence. *Behavioral and Brain Sciences*, 53(2), 90–93. DOI:10.1016/j.paid.2011.05.015

Burt de Perera, T., Holbrook, R. I., & Davis, V. (2016). The representation of three-dimensional space in fish. *Frontiers in Behavioral Neuroscience*, 10, 40. DOI:10.3389/fnbeh.2016.00040

Butler, P. J. (2016). The physiological basis of bird flight. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1704), 20150384. DOI:10.1098/rstb.2015.0384

Buzsáki, G., & Moser, E. I. (2013). Memory, navigation and theta rhythm in the hippocampal-entorhinal system. *Nature Neuroscience*, 16(2), 130–138. DOI:10.1038/nn.3304

Byrne, R. W. (1979). Memory for urban geography. *Quarterly Journal of Experimental Psychology*, 31(1), 147–154. DOI:10.1080/14640747908400714

Byrne, R. W. (1996). Relating brain size to intelligence. In P. A. Mellars & K. R. Gibson (Eds.), *Modelling the early human mind* (pp. 49–56). Cambridge, UK: McDonald Institute for Archaeological Research.

Byrne, R. W. (2000). How monkeys find their way: leadership, coordination, and cognitive maps of African baboons. In Sue Boinski & P. A. Garber (Eds.), *On the move: how and why animals travel in groups* (pp. 491–518). Chicago, US: University of Chicago Press.

Byrne, R. W., Noser, R., Bates, L. A., & Jupp, P. E. (2009). How did they get here from there? Detecting changes of direction in terrestrial ranging. *Animal Behaviour*, 77(3), 619–631. DOI:10.1016/J.ANBEHAV.2008.11.014

Caillaud, D., Ndagijimana, F., Giarrusso, A. J., Vecellio, V., & Stoinski, T. S. (2014). Mountain gorilla ranging patterns: influence of group size and group dynamics. *American Journal of Primatology*, 76(8), 730–746. DOI:10.1002/ajp.22265

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519. DOI:10.1016/j.ecolmodel.2006.03.017

Caro, T. (2007). Behavior and conservation: a bridge too far? *Opinion TRENDS in Ecology and Evolution*, 22(8). DOI:10.1016/j.tree.2007.06.003

Carpenter, C. R. (1934). A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). In C. R. Carpenter (Ed.), *Naturalistic behavior of nonhuman primates* (pp. 3–92). US, Pennsylvania: Pennsylvania State University Press.

Carvalho, L. S., Pessoa, D. M. A., Mountford, J. K., Davies, W. I. L., & Hunt, D. M. (2017). The genetic and evolutionary drives behind primate color vision. *Frontiers in Ecology and Evolution*, 5, 34. DOI:10.3389/fevo.2017.00034

Cavada, N., Ciolli, M., Barelli, C., & Rovero, F. (2017). Optimizing field and analytical procedures for estimating densities of arboreal and threatened primates in tropical rainforest. *American Journal of Primatology*, 79(9), e22666. DOI:10.1002/ajp.22666

Cavada, N., Ciolli, M., Rocchini, D., Barelli, C., Marshall, A. R., & Rovero, F. (2017). Integrating field and satellite data for spatially explicit inference on the density of threatened arboreal primates. *Ecological Applications*, 27(1), 235–243. DOI:10.1002/eap.1438

Ceccarelli, E., Rangel Negrín, A., Coyohua-Fuentes, A., Canales-Espinosa, D., Américo Dias, P. D., & Setchell, J. M. (2019). An exploration of the factors influencing the spatial behavior of mantled howler monkeys (Alouatta palliata). *International Journal of Primatology*, 40(2), 197–213. DOI:10.1007/s10764-018-0075-1

Chapman, C. A., Chapman, L. J., Kaufman, L., & Zanne, A. E. (1999). Potential causes of arrested succession in Kibale National Park, Uganda: Growth and mortality of seedlings. *African Journal of Ecology*, 37(1), 81–92. DOI:10.1046/j.1365-2028.1999.00159.x

Chapman, C. A., Chapman, L. J., Rode, K. D., Hauck, E. M., & McDowell, L. R. (2003). Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology*, 24(2), 317–333. DOI:10.1023/A:1023049200150

Chapman, C. A., Wrangham, R. W., Chapman, L. J., Kennard, D. K., & Zanne, A. E. (1999). Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*, 15(2), 189–211. DOI:10.1017/S0266467499000759

Charnov, E. L. (1976). Optimal foraging: the marginal value theorem. *Theoretical Population Biology*, 9, 129–136.

Cheeseman, J. F., Millar, C. D., Greggers, U., Lehmann, K., Pawley, M. D. M., Gallistel, C. R., … Menzel, R. (2014). Way-finding in displaced clock-shifted bees proves bees use a cognitive map. *Proceedings of the National Academy of Sciences of the United States of America*, 111(24), 8949–8954. DOI:10.1073/pnas.1408039111

Cheng, K., & Spetch, M. L. (1998). Mechanisms of landmark use in mammals and birds. In S. Healy (Ed.), *Spatial representation in animals* (pp. 1–17). Oxford University Press.

Chivers, D. J., & Hladik, C. M. (1980). Morphology of the gastrointestinal tract in primates : comparisons with other mammals in relation to diet. *Journal of Morphology*, 166, 337–386.

Clayton, N. S. (2017). Episodic-like memory and mental time travel in animals. In J. Call, G. M. Burghardt, I. M. Pepperberg, C. T. Snowdon, & T. Zentall (Eds.), *APA handbook of comparative psychology: Perception, learning, and cognition.* (pp. 227–243). DOI:10.1037/0000012-011

Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, 395(6699), 272–274. DOI:10.1038/26216

Clutton-Brock, T. H., & Harvey, P. H. (1980). Primates, brains and ecology. *Journal of Zoology*, 190, 309–323.

Collett, M., & Collett, T. S. (2000). How do insects use path integration for their navigation? *Biological Cybernetics*, 83(3), 245–259. DOI:10.1007/s004220000168

Collett, T. S., Cartwright, B. A., & Smith, B. A. (1986). Landmark learning and visuo-spatial memories in gerbils. *Journal of Comparative Physiology A Sensory, Neural, and Behavioral Physiology*, 158(6), 835–851. DOI:10.1007/BF01324825

Collett, Thomas S., & Graham, P. (2004). Animal navigation: path integration, visual landmarks and cognitive maps. *Current Biology*, 14(12), R475–R477. DOI:10.1016/j.cub.2004.06.013

CONAGUA. (2019). *Resúmenes mensuales de lluvia y temperatura de la comisión nacional del agua, Mexico.*

Corballis, M. C. (2019). Mental time travel, language, and evolution. *Neuropsychologia*, 134, 107202. DOI:10.1016/j.neuropsychologia.2019.107202

Cortés-Ortiz, L. (2017). Hybridization and hybrid zones. In A. Fuentes (Ed.), *The international encyclopedia of primatology* (pp. 1–5). DOI:10.1002/9781119179313.wbprim0380

Côrtes, M. C., & Uriarte, M. (2013). Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal. *Biological Reviews*, 88(2), 255–272. DOI:10.1111/j.1469-185X.2012.00250.x

Couzin, I. D. (2009). Collective cognition in animal groups. *Trends in Cognitive Sciences*, 13(1), 36–43. DOI:10.1016/J.TICS.2008.10.002

Cozzi, G., Broekhuis, F., McNutt, J. W., Turnbull, L. A., Macdonald, D. W., & Schmid, B. (2012). Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. *Ecology*, 93(12), 2590–2599. DOI:10.1890/12-0017.1

Crête, M., & Larivière, S. (2003). Estimating the costs of locomotion in snow for coyotes. *Canadian Journal of Zoology*, 81(11), 1808–1814. DOI:10.1139/z03-182

Crystal, J. D. (2016). Animal models of source memory. *Journal of the Experimental Analysis of Behaviour*, 105(1), 56–67. DOI:10.1002/jeab.173

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *International Journal of Complex Systems*, 1695(5), 1–9.

Cunningham, E. P., & Janson, C. H. (2013). Effect of fruit scarcity on use of spatial memory in a seed predator, white-faced Saki (*Pithecia pithecia*). *International Journal of Primatology*, 34(4), 808–822. DOI:10.1007/s10764-013-9697-5

Cushman, S. A. (2010). Animal movement data: GPS telemetry, autocorrelation and the need for path-level analysis. In S. A. Cushman & F. Huettmann (Eds.), *Spatial complexity, informatics, and wildlife conservation* (pp. 131–149). DOI:10.1007/978-4-431-87771-4_7

Dacke, M., Baird, E., Byrne, M., Scholtz, C. H., & Warrant, E. J. (2013). Dung beetles use the milky way for orientation. *Current Biology*, 23(4), 298–300. DOI:10.1016/j.cub.2012.12.034

Darwin, C. (1859). *On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life* (J. Murray, Ed.). London.

Dasen, P. R. (1984). The cross-cultural study of intelligence: Piaget and the Baoule. *International Journal of Psychology*, 19, 407–434.

Davidson, G. L., Cooke, A. C., Johnson, C. N., & Quinn, J. L. (2018). The gut microbiome as a driver of individual variation in cognition and functional behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1756), 20170286. DOI:10.1098/rstb.2017.0286

Davies, A. B., Ancrenaz, M., Oram, F., & Asner, G. P. (2017). Canopy structure drives orangutan habitat selection in disturbed Bornean forests. *Proceedings of the Natural Academy of Science*, 114(31), 8307–8312. DOI:10.1073/pnas.1706780114

De Raad, A. L., & Hill, R. A. (2019). Topological spatial representation in wild chacma baboons (*Papio ursinus*). *Animal Cognition*, 22(3), 397–412. DOI:10.1007/s10071-019-01253-6

de Waal, F. B. M., & Ferrari, P. F. (2010). Towards a bottom-up perspective on animal and human cognition. *Trends in Cognitive Sciences*, 14(5), 201–207. DOI:10.1016/j.tics.2010.03.003

Deaner, R. O., Isler, K., Burkart, J., & van Schaik, C. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior and Evolution*, 70(2), 115–124. DOI:10.1159/000102973

Deaner, R. O., van Schaik, C. P., & Johnson, V. (2006). Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evolutionary Psychology*, 4(1), 149–196.

DeCasien, A. R., & Higham, J. P. (2019). Primate mosaic brain evolution reflects selection on sensory and cognitive specialization. *Nature Ecology and Evolution*, 3(10), 1483–1493. DOI:10.1038/s41559-019-0969-0

DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology and Evolution*, 1(5), 1–7. DOI:10.1038/s41559-017-0112

Delgado, M. del M., Miranda, M., Alvarez, S. J., Gurarie, E., Fagan, W. F., Penteriani, V., … Morales, J. M. (2018). The importance of individual variation in the dynamics of animal collective movements. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1746), 20170008. DOI:10.1098/rstb.2017.0008

Delgado, M. M., & Jacobs, L. F. (2017). Caching for where and what: evidence for a mnemonic strategy in a scatter-hoarder. *Royal Society Open Science*, 4(9), 170958. DOI:10.1098/rsos.170958

Denny, C. K., Stenhouse, G. B., & Nielsen, S. E. (2018). Scales of selection and perception: landscape heterogeneity of an important food resource influences habitat use by a large omnivore. *Wildlife Biology*, 2018(1), 1–10. DOI:10.2981/wlb.00409

Di Fiore, A., Link, A., & Campbell, C. J. (2011). The atelines: behavioral and socioecological diversity in a New World monkey radiation. In C. J. Campbell, A. Fuentes, M. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (pp. 155–188). New York: Oxford University Press.

Di Fiore, Anthony, & Suarez, S. A. (2007). Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. *Animal Cognition*, 10(3), 317–329. DOI:10.1007/s10071-006-0067-y

Dias, P. A., & Rangel-Negrín, A. (2015). Diets of howler monkeys. In M.M. Kowalewski, P. A. Garber, L. Cortes-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behavior, ecology, and conservation* (pp. 21–56). DOI:10.1007/978-1-4939-1960-4_2

Diaz-Gallegos, J. R. (1996). *Estructura y composición florística del Parque Nacional zona arqueológica de Palenque, Chiapas, Mexico*. Universidad Juárez Autónoma de Tabasco.

Dicke, U., & Roth, G. (2016). Neuronal factors determining high intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1685), 20150180. DOI:10.1098/rstb.2015.0180

Doherty, T. S., & Driscoll, D. A. (2018). Coupling movement and landscape ecology for animal conservation in production landscapes. *Proceedings of the Royal Society B: Biological Sciences*, 285(1870), 20172272. DOI:10.1098/rspb.2017.2272

Dolins, F. L., Schweller, K., & Milne, S. (2017). Technology advancing the study of animal cognition: using virtual reality to present virtually simulated environments to investigate nonhuman primate spatial cognition. *Current Zoology*, 63(1), 97–108. DOI:10.1093/cz/zow121

Dominy, N. J., & Lucas, P. W. (2001). Ecological importance of trichromatic vision to primates. *Nature*, 410(6826), 363–366. DOI:10.1038/35066567

Dukas, R. (2004). Evolutionary biology of animal cognition. *Annual Review of Ecology, Evolution, and Systematics*, 35(1), 347–374. DOI:10.1146/annurev.ecolsys.35.112202.130152

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science*, 317(5843), 1344–1347. DOI:10.1126/science.1145463

Dunn, J. C., Cristóbal-Azkarate, J., & Veà, J. J. (2010). Seasonal variations in the diet and feeding effort of two groups of howlers in different sized forest fragments. *International Journal of Primatology*, 31(5), 887–903. DOI:10.1007/s10764-010-9436-0

Dyer, F. C. (2000). Group movement and individual cognition: lessons from social insects. In Sue Boinski & P. A. Garber (Eds.), *On the move: how and why animals travel in groups* (pp. 127–164). Chicago, US: University of Chicago Press.

Eichenbaum, H., Dudchenko, P., Wood, E., Shapiro, M., & Tanila, H. (1999). The hippocampus, memory, and place cells: Is it spatial memory or a memory space? *Neuron*, 23(2), 209–226. DOI:10.1016/S0896-6273(00)80773-4

Emery, N. J., & Clayton, N. S. (2004). Comparing the complex cognition of birds and primates. In L. J. Rogers & G. Kaplan (Eds.), *Comparative vertebrate cognition* (pp. 3–55). DOI:10.1007/978-1-4419-8913-0_1

Emlen, S. T. (1975). The stellar-orientation system of a migratory bird. *Scientific American*, 233, 102–111. DOI:10.2307/24949869

English, M., Ancrenaz, M., Gillespie, G., Goossens, B., Nathan, S., & Linklater, W. (2014). Foraging site recursion by forest elephants *Elephas maximus borneensis*. *Current Zoology*, 60(4), 551–559. DOI:10.1093/CZOOLO/60.4.551

Estrada, A., & Coates-Estrada, R. (1984). Fruit eating and seed dispersal by howling monkeys (Alouatta palliata) in the tropical rain forest of Los Tuxtlas, Mexico. *American Journal of Primatology*, 6(2), 77–91. DOI:10.1002/ajp.1350060202

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., … Li, B. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, 3(1), e1600946. DOI:10.1126/sciadv.1600946

Estrada, A., Mendoza, A., Castellanos, L., Pacheco, R., Van Belle, S., García, Y., & Muñoz, D. (2002). Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, Mexico. *American Journal of Primatology*, 58(2), 45–55. DOI:10.1002/ajp.10051

Etienne, A. S., & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus*, 14(2), 180–192. DOI:10.1002/hipo.10173

Fagan, W. F., Gurarie, E., Bewick, S., Howard, A., Cantrell, R. S., & Cosner, C. (2017). Perceptual ranges, information gathering, and foraging success in dynamic landscapes. *The American Naturalist*, 189(5), 474–489. DOI:10.1086/691099

Fagan, W. F., Lewis, M. A., Auger-M Eth, M., Avgar, T., Benhamou, S., Breed, G., … Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters*, 16, 1316–1329. DOI:10.1111/ele.12165

Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, 21(6), 1003–1015. DOI:10.1111/j.1365-2435.2007.01326.x

Fawcett, T. W., Marshall, & Higginson, J. A. R. (2015). The evolution of mechanisms underlying behaviour. *Current Zoology*, 61(2), 221–225.

Feng, J. J., Cui, L. W., Ma, C. Y., Fei, H. L., & Fan, P. F. (2014). Individuality and stability in male songs of cao vit gibbons (*Nomascus nasutus*) with potential to monitor population dynamics. *PLoS ONE*, 9(5), e96317. DOI:10.1371/journal.pone.0096317

Figueroa, F., & Sánchez-Cordero, V. (2008). Effectiveness of natural protected areas to prevent land use and land cover change in Mexico. *Biodiversity and Conservation*, 17(13), 3223–3240. DOI:10.1007/s10531-008-9423-3

Fishlock, V., Caldwell, C., & Lee, P. C. (2016). Elephant resource-use traditions. *Animal Cognition*, 19(2), 429–433. DOI:10.1007/s10071-015-0921-x

Fleming, T. H., & Murray, K. L. (2009). Population and genetic consequences of hurricanes for three species of west Indian phyllostomid bats. *Biotropica*, 41(2), 250–256. DOI:10.1111/j.1744-7429.2008.00466.x

Fontaine, B., Moisson, P. Y., & Wickings, E. J. (1995). Observations of spontaneous tool making and tool use in a captive group of western lowland gorillas (*Gorilla gorilla gorilla*). *Folia Primatologica*, 65(4), 219–223.

Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map versus landmark-based navigation of novel shortcuts. *Journal of Experimental Psychology: Learning Memory and Cognition*, 31(2), 195–215. DOI:10.1037/0278-7393.31.2.195

Ford, S. M. (2006). The biogeographic history of Mesoamerican primates. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. G. Luecke (Eds.), *New perspectives in the study of Mesoamerican primates: distribution, ecology, and conservation* (pp. 81–114). DOI:DOI:10.1007/0-387-25872-8_15

Fortes, V. B., Bicca-Marques, J. C., Urbani, B., Fernández, V. A., & Da Silva Pereira, T. (2015). Ranging behavior and spatial cognition of howler monkeys. In M.M. Kowalewski, P. A. Garber, L. Cortes-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behavior, ecology, and conservation* (pp. 219–255). DOI:10.1007/978-1-4939-1960-4_9

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86(5), 1320–1330. DOI:10.1890/04-0953

Fox, J., & Weisberg, S. (2011). Multivariate linear models in R. In H. Salmon, O'HeffernanM., K. DeRosa, & G. Dickens (Eds.), *An R companion to applied regression*. Los Angeles: SAGE Publications.

Fürtbauer, I., Mundry, R., Heistermann, M., Schülke, O., & Ostner, J. (2011). You mate, I mate: macaque females synchronize sex not cycles. *PLoS ONE*, 6(10), e26144. DOI:10.1371/journal.pone.0026144

Gabi, M., Collins, C. E., Wong, P., Torres, L. B., Kaas, J. H., & Herculano-Houzel, S. (2010). Cellular scaling rules for the brains of an extended number of primate species. *Brain, Behavior and Evolution*, 76(1), 32–44. DOI:10.1159/000319872

Galán-Acedo, C., Arroyo-Rodríguez, V., Estrada, A., & Ramos-Fernández, G. (2019). Forest cover and matrix functionality drive the abundance and reproductive success of an endangered primate in two fragmented rainforests. *Landscape Ecology*, 34(1), 147–158. DOI:10.1007/s10980-018-0753-6

Gale, N., Golledge, R. G., Pellegrino, J. W., & Doherty, S. (1990). The acquisition and integration of route knowledge in an unfamiliar neighborhood. *Journal of Environmental Psychology*, 10(1), 3–25. DOI:10.1016/S0272-4944(05)80021-0

Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: The MIT Press.

Gallotti, R., Porter, M. A., & Barthelemy, M. (2016). Lost in transportation: information measures and cognitive limits in multilayer navigation. *Science Advances*, 2(2), e1500445. DOI:10.1126/sciadv.1500445

Ganas, J., & Robbins, M. M. (2004). Intrapopulation differences in ant eating in the mountain gorillas of Bwindi Impenetrable National Park, Uganda. *Primates*, 45(4), 275–278. DOI:10.1007/s10329-004-0089-5

Garber, P. A. (2000). Evidence for the use of spatial, temporal, and social information by some primate foragers. In Sue Boinski & P. A. Garber (Eds.), *On the move: how and why animals travel in groups* (pp. 261–298). Chicaco, US: University of Chicago Press.

Garber, P. A., & Bicca-Marques, J. C. (2002). *Eat or be eaten: predator sensitive foraging among primates* (L. E. Miller, Ed.). Cambridge, UK: Cambridge University Press.

Garber, P. A., & Brown, E. (2006). Use of landmark cues to locate feeding sites in wild capuchin monkeys (Cebus capucinus): an experimental field study. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of mesoamerican primates* (pp. 311–332). DOI:10.1007/0-387-25872-8_15

Garber, P. A., & Dolins, F. L. (2014). Primate spatial strategies and cognition: introduction to this special issue. *American Journal of Primatology*, 76(5), 393–398. DOI:10.1002/ajp.22257

Garber, P. A., & Hannon, B. (1993). Modeling monkeys: a comparison of computer-generated and naturally occurring foraging patterns in two species of neotropical primates. *International Journal of Primatology*, 14(6), 827–852. DOI:10.1007/BF02220255

Garber, P. A., & Jelinek, P. E. (2006). Travel patterns and spatial mapping in Nicaraguan mantled howler monkeys (*Alouatta palliata*). In A. Estrada, P. A. Garber, M. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of mesoamerican primates.* (pp. 287–309). DOI:DOI:10.1007/0-387-25872-8_15

Garber, P. A., & Porter, L. M. (2014). Navigating in small-scale space: The role of landmarks and resource monitoring in understanding saddleback tamarin travel. *American Journal of Primatology*, 76(5), 447–459. DOI:10.1002/ajp.22196

Gardner, R. J., & Moser, M.-B. (2017). Multiple mechanisms for memory replay? *Science*, 355(6321), 131–132. DOI:10.1126/science.aam5404

Gastner, M. T., & Newman, M. E. J. (2006). The spatial structure of networks. *European Physical Journal B*, 49(2), 247–252. DOI:10.1140/epjb/e2006-00046-8

Gautestad, A. O. (2011). Memory matters: influence from a cognitive map on animal space use. *Journal of Theoretical Biology*, 287(1), 26–36. DOI:10.1016/j.jtbi.2011.07.010

Gautestad, A. O., Loe, L. E., & Mysterud, A. (2013). Inferring spatial memory and spatiotemporal scaling from GPS data: comparing red deer *Cervus elaphus* movements with simulation models. *Journal of Animal Ecology*, 82(3), 572–586. DOI:10.1111/1365-2656.12027

Gomes, D. G. E., Page, R. A., Geipel, I., Taylor, R. C., Ryan, M. J., & Halfwerk, W. (2016). Bats perceptually weight prey cues across sensory systems when hunting in noise. *Science*, 353(6305), 1277–1280. DOI:10.1126/science.aaf7934

Gómez-Dominguez, H., Farrera, M. A. P., Jimenez, J. A. E., & Reynoso, M. I. M. (2015). Listado florístico del Parque Nacional Palenque, Chiapas, México. *Botanical Sciences*, 93(3), 559–578. DOI:10.17129/botsci.151

Gómez, J. M., & Verdú, M. (2012). Mutualism with plants drives primate diversification. *Systematic Biology*, 61(4), 567–577. DOI:10.5061/DRYAD.KH21QB76

González-Forero, M., & Gardner, A. (2018). Inference of ecological and social drivers of human brain-size evolution. *Nature*, 557(7706), 554–557. DOI:10.1038/s41586-018-0127-x

González-Gómez, P. L., Bozinovic, F., & Vásquez, R. A. (2011). Elements of episodic-like memory in free-living hummingbirds, energetic consequences. *Animal Behaviour*, 81(6), 1257–1262. DOI:10.1016/J.ANBEHAV.2011.03.014

Gouveia, S. F., Villalobos, F., Dobrovolski, R., Beltraõ-Mendes, R., & Ferrari, S. F. (2014). Forest structure drives global diversity of primates. *Journal of Animal Ecology*, 83(6), 1523–1530. DOI:10.1111/1365-2656.12241

Gregory, T., Mullett, A., & Norconk, M. A. (2014). Strategies for navigating large areas: A GIS spatial ecology analysis of the bearded saki monkey, *Chiropotes sagulatus*, in Suriname. *American Journal of Primatology*, 76(6), 586–595. DOI:10.1002/ajp.22251

Griffiths, D., Dickinson, A., & Clayton, N. (1999). Episodic memory: what can animals remember about their past? *Trends in Cognitive Sciences*, 3(2), 74–80. DOI:10.1016/S1364-6613(98)01272-8

Guerra, P. A., & Reppert, S. M. (2013). Coldness triggers northward flight in remigrant monarch butterflies. *Current Biology*, 23(5), 419–423. DOI:10.1016/j.cub.2013.01.052

Guilford, T., & Biro, D. (2014). Route following and the pigeon's familiar area map. *The Journal for Experimental Biology*, 217(2), 169–179. DOI:10.1242/jeb.092908

Guilford, T., & Taylor, G. K. (2014). The sun compass revisited. *Animal Behaviour*, 97, 135–143. DOI:10.1016/j.anbehav.2014.09.005

Hahn, U. (2011). The problem of circularity in evidence, argument, and explanation. *Perspectives on Psychological Science*, 6(2), 172–182. DOI:10.1177/1745691611400240

Halsey, L. G. (2016). Terrestrial movement energetics: current knowledge and its application to the optimising animal. *Journal of Experimental Biology*, 219(10), 1424–1431. DOI:10.1242/jeb.133256

Halsey, L. G., & White, C. R. (2017). A different angle: comparative analyses of whole-animal transport costs when running uphill. *Journal of Experimental Biology*, 220(2), 161–166. DOI:10.1242/jeb.142927

Hardus, M. E., Lameira, A. R., Zulfa, A., Atmoko, S. S. U., de Vries, H., & Wich, S. A. (2012). Behavioral, ecological, and evolutionary aspects of meat-eating by Sumatran Orangutans (*Pongo abelii*). *International Journal of Primatology*, 33(2), 287–304. DOI:10.1007/s10764-011-9574-z

Hart, B. L., Hart, L. A., & Pinter-Wollman, N. (2008). Large brains and cognition: where do elephants fit in? *Neuroscience and Biobehavioral Reviews*, 32(1), 86–98. DOI:10.1016/j.neubiorev.2007.05.012

Harten, L., Katz, A., Goldshtein, A., Handel, M., & Yovel, Y. (2020). The ontogeny of a mammalian cognitive map in the real world. *Science*, 197(July), 194–197.

Haun, D. B. M., Rapold, C. J., Call, J., Janzen, G., & Levinson, S. C. (2006). Cognitive cladistics and cultural override in Hominid spatial cognition. *Proceedings of the National Academy of Sciences*, 103(46), 17568–17573. DOI:10.1073/pnas.0607999103

Haun, D. B. M., Rapold, C. J., Janzen, G., & Levinson, S. C. (2011). Plasticity of human spatial cognition: spatial language and cognition covary across cultures. *Cognition*, 119(1), 70–80. DOI:10.1016/j.cognition.2010.12.009

Heise-Pavlov, S. R., Jackrel, S. L., & Meeks, S. (2011). Conservation of a rare arboreal mammal: habitat preferences of the Lumholtz's tree-kangaroo, *Dendrolagus lumholtzi*. *Australian Mammalogy*, 33(1), 5–12. DOI:10.1071/AM09036

Henke, S. (2007). Disease emergence and resurgence: the wildlife–human connection. *Journal of Wildlife Management*, 71(1), 293–293. DOI:10.2193/2006-514

Herculano-Houzel, S. (2009). The human brain in numbers: a linearly scaled-up primate brain. *Frontiers in Human Neuroscience*, 3, 31. DOI:10.3389/neuro.09.031.2009

Herculano-Houzel, S. (2011). Not all brains are made the same: new views on brain scaling in evolution. *Brain, Behavior and Evolution*, 78(1), 22–36. DOI:10.1159/000327318

Hernández Salazar, L. T., Dominy, N. J., & Laska, M. (2015). The sensory systems of Alouatta: evolution with an eye to ecology. In M.M. Kowalewski, P. A. Garber, L. Cortes-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behavior, ecology, and conservation* (pp. 317–336). DOI:10.1007/978-1-4939-1957-4_12

Herrmann, E., Hare, B., Call, J., & Tomasello, M. (2010). Differences in the cognitive skills of bonobos and chimpanzees. *PLoS ONE*, 5(8). DOI:10.1371/journal.pone.0012438

Hobaiter, C., & Byrne, R. W. (2014). The meanings of chimpanzee gestures. *Current Biology*, 24(14), 1596–1600. DOI:10.1016/j.cub.2014.05.066

Hobaiter, C., Byrne, R. W., & Zuberbühler, K. (2017). Wild chimpanzees' use of single and combined vocal and gestural signals. *Behavioral Ecology and Sociobiology*, 71(6), 1–13. DOI:10.1007/s00265-017-2325-1

Hohmann, G., Fowler, A., Sommer, V., & Ortmann, S. (2006). Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: the influence of abundance and nutritional quality of fruit. In G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding ecology in Apes and other Primates* (pp. 123–159). Cambridge, UK: Cambridge University Press.

Holland, R. A., Thorup, K., Vonhof, M. J., Cochran, W. W., & Wikelski, M. (2006). Bat orientation using Earth's magnetic field. *Nature*, 444(7120), 702.

DOI:10.1038/444702a

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., & Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences*, 105(49), 19060–19065. DOI:10.1073/pnas.0800483105

Holzmann, I., & Areta, J. I. (2020). Reduced geographic variation in roars in different habitats rejects the acoustic adaptation hypothesis in the black-and-gold howler monkey (*Alouatta caraya*). *Ethology*, 126(1), 76–87. DOI:10.1111/eth.12962

Hopkins, M. E. (2011). Mantled howler (*Alouatta palliata*) arboreal pathway networks: relative impacts of resource availability and forest structure. *International Journal of Primatology*, 32(1), 238–258. DOI:10.1007/s10764-010-9464-9

Hopkins, M. E. (2013). Relative dominance and resource availability mediate Mantled Howler (*Alouatta palliata*) spatial responses to neighbors' loud calls. *International Journal of Primatology*, 34(5), 1032–1054. DOI:10.1007/s10764-013-9713-9

Hopkins, M. E. (2016). Mantled howler monkey spatial foraging decisions reflect spatial and temporal knowledge of resource distributions. *Animal Cognition*, 19(2), 387–403. DOI:10.1007/s10071-015-0941-6

Hopkins, W. D., Lyn, H., & Cantalupo, C. (2009). Volumetric and lateralized differences in selected brain regions of chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). *American Journal of Primatology*, 71(12), 988–997. DOI:10.1002/ajp.20741

Houle, A., Chapman, C. A., & Vickery, W. L. (2007). Intratree variation in fruit production and implications for primate foraging. *International Journal of Primatology*, 28(6), 1197–1217. DOI:10.1007/s10764-007-9214-9

Howard, A. M., Gurarie, E., Visalberghi, E., Izar, P., Fragaszy, D., & Fagan, W. (2019). The environment beyond points of directional change. *American Journal of Physical Anthropology*, 168, 109–110.

Howard, A. M., Mainali, K., Fagan, W. F., Visalberghi, E., Izar, P., Jones, C., & Fragaszy, D. (2018). Foraging and inter-individual distances of bearded capuchin monkeys. *American Journal of Primatology*, 80(8), e22900. DOI:10.1002/ajp.22900

Howard, Allison M., Nibbelink, N. P., Madden, M., Young, L. A., Bernardes, S., & Fragaszy, D. M. (2015). Landscape influences on the natural and artificially manipulated movements of bearded capuchin monkeys. *Animal Behaviour*, 106, 59–70. DOI:10.1016/J.ANBEHAV.2015.05.003

Iachini, T., Ruotolo, F., & Ruggiero, G. (2009). The effects of familiarity and gender on spatial representation. *Journal of Environmental Psychology*, 29(2), 227–234. DOI:10.1016/j.jenvp.2008.07.001

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 111(2), 159–173. DOI:10.1037/0735-7036.111.2.159

Isbell, L. A., Bidner, L. R., Van Cleave, E. K., Matsumoto-Oda, A., & Crofoot, M. C. (2018). GPS-identified vulnerabilities of savannah-woodland primates to leopard predation and their implications for early hominins. *Journal of Human Evolution*, 118, 1–13. DOI:10.1016/j.jhevol.2018.02.003

Isbell, L. A., & Young, T. P. (1996). The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. *Journal of Human Evolution*, 30(5), 389–397. DOI:10.1006/jhev.1996.0034

Isler, K., & van Schaik, C. P. (2006). Metabolic costs of brain size evolution. *Biology Letters*, 2(4), 557–560. DOI:10.1098/rsbl.2006.0538

Jacobs, G. H., Neitzt, M., Deegan, J. F., & Neitzt, J. (1996). Trichromatic colour vision in New World monkeys. *Nature*, 382, 156–158.

Jacobs, L. F., & Menzel, R. (2014). Navigation outside of the box: what the lab can learn from the field and what the field can learn from the lab. *Movement Ecology*, 2(1), 3. DOI:10.1186/2051-3933-2-3

Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: the parallel map theory of hippocampal function. *Psychological Review*, 110(2), 285–315.

Jacoby, D. M. P., Brooks, E. J., Croft, D. P., & Sims, D. W. (2012). Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. *Methods in Ecology and Evolution*, 3(3), 574–583. DOI:10.1111/J.2041-210X.2012.00187.X@10.1111/(ISSN)2041-210X.AWARDS2012

Jacoby, D. M. P., & Freeman, R. (2016). Emerging network-based tools in movement ecology 1. *Trends in Ecology & Evolution*, 31(4), 301–314.

Jang, H., Boesch, C., Mundry, R., Ban, S. D., & Janmaat, K. R. L. (2019). Travel linearity and speed of human foragers and chimpanzees during their daily search for food in tropical rainforests. *Scientific Reports*, 9(11066), 1–13. DOI:10.1038/s41598-019-47247-9

Jang, H., Boesch, C., Mundry, R., Kandza, V., & Janmaat, K. R. L. (2019). Sun, age and test location affect spatial orientation in human foragers in rainforests. *Proceedings of the Royal Society B: Biological Sciences*, 289(1907), 20190934. DOI:10.1098/rspb.2019.0934

Janmaat, K. R. L. (2019). What animals do not do or fail to find: a novel observational approach for studying cognition in the wild. *Evolutionary Anthropology: Issues, News, and Reviews*, 28(6), 303–320. DOI:10.1002/evan.21794

Janmaat, K. R. L., Ban, S. D., & Boesch, C. (2013). Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. *Animal Behaviour*, 86(6), 1183–1205. DOI:10.1016/j.anbehav.2013.09.021

Janmaat, K. R. L., Boesch, C., Byrne, R. W., Chapman, C. A., Goné Bi, Z. B., Head, J. S., … Polansky, L. (2016). Spatio-temporal complexity of chimpanzee food: how cognitive adaptations can counteract the ephemeral nature of ripe fruit. *American*

Journal of Primatology, 78(6), 626–645. DOI:10.1002/ajp.22527

Janmaat, K. R. L., Chapman, C. A., Meijer, R., & Zuberbühler, K. (2012). The use of fruiting synchrony by foraging mangabey monkeys: a 'simple tool' to find fruit. *Animal Cognition*, 15(1), 83–96. DOI:10.1007/s10071-011-0435-0

Janmaat, K. R. L., Polansky, L., Ban, S. D., & Boesch, C. (2014). Wild chimpanzees plan their breakfast time, type, and location. *Proceedings of the National Academy of Sciences*, 111(46), 16343–16348. DOI:10.1073/pnas.1407524111

Janson, C.H. (2014). Death of the (traveling) salesman: Primates do not show clear evidence of multi-step route planning. *American Journal of Primatology*, 76(5), 410–420. DOI:10.1002/ajp.22186

Janson, Charles H. (2016). Capuchins, space, time and memory: an experimental test of what-where-when memory in wild monkeys. *Proceedings of the Royal Society B: Biological Sciences*, 283(1840), 20161432. DOI:10.1098/rspb.2016.1432

Janson, Charles H. (2019). Foraging benefits of ecological cognition in fruit-eating primates: results from field experiments and computer simulations. *Frontiers in Ecology and Evolution*, 7(125), 1–8. DOI:10.3389/fevo.2019.00125

Janson, Charles H., & Bitetti, M. S. D. (1997). Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. *Behavioral Ecology and Sociobiology*, 41(1), 17–24. DOI:10.1007/s002650050359

Janson, Charles H., & Byrne, R. W. (2007). What wild primates know about resources: opening up the black box. *Animal Cognition*, 10(3), 357–367. DOI:10.1007/s10071-007-0080-9

Janson, Charles H., & Chapman, C. A. (1999). Resources and primate community structure. In J. G. Fleagle, C. H. Janson, & K. Reed (Eds.), *Primate Communities* (pp. 237–250). Cambridge, UK: Cambridge University Press.

Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., … Bauer, S. (2013). Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology*, 1(1), 1–13. DOI:10.1186/2051-3933-1-6

Jerison, H. J. (1970). Brain evolution: new light on old principles. *Science*, 170, 1224–1225. DOI:10.1126/science.170.3963.1224

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., … Kauffman, M. J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science*, 316(6406), 1023–1025.

Johnson, S. D., & Nicolson, S. W. (2008). Evolutionary associations between nectar properties and specificity in bird pollination systems. *Biology Letters*, 4(1), 49–52. DOI:10.1098/rsbl.2007.0496

Joly, M., & Zimmermann, E. (2011). Do solitary foraging nocturnal mammals plan their routes? *Biology Letters*, 7(4), 638–640. DOI:10.1098/rsbl.2011.0258

Kareiva, R. M., & Shigesada, N. (1983). Analyzing insect movement as a correlated random walk. *Oecologia*, 56, 234–238. DOI:0029-8549/83/0056/0234

Kemink, K. M., & Kesler, D. C. (2013). Using movement ecology to inform translocation efforts: a case study with an endangered lekking bird species. *Animal Conservation*, 16(4), 449–457. DOI:10.1111/acv.12015

Killian, N. J., Jutras, M. J., & Buffalo, E. A. (2012). A map of visual space in the primate entorhinal cortex. *Nature*, 491(7426), 761–764. DOI:10.1038/nature11587

Kittle, A. M., Bukombe, J. K., Sinclair, A. R. E., Mduma, S. A. R., & Fryxell, J. M. (2015). Landscape-level movement patterns by lions in western Serengeti: comparing the influence of inter-specific competitors, habitat attributes and prey availability. *Movement Ecology*, 4(1), 1–17. DOI:10.1186/s40462-016-0082-9

Klein, S. B., Robertson, T. E., & Delton, A. W. (2010). Facing the future: memory as an evolved system for planning future acts. *Memory and Cognition*, 38(1), 13–22. DOI:10.3758/MC.38.1.13

Korine, C., & Kalko, E. K. V. (2005). Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction. *Behavioral Ecology and Sociobiology*, 59(1), 12–23. DOI:10.1007/s00265-005-0003-1

Korstjens, A. H., Lehmann, J., & Dunbar, R. I. M. (2010). Resting time as an ecological constraint on primate biogeography. *Animal Behaviour*, 79(2), 361–374. DOI:10.1016/j.anbehav.2009.11.012

Kowalewski, M.M., & Raño, M. (2017). Howler Monkey (Alouatta). In *The International Encyclopedia of Primatology* (pp. 1–3). DOI:10.1002/9781119179313.wbprim0184

Krasnow, M. M., Truxaw, D., Gaulin, S. J. C., New, J., Ozono, H., Uono, S., … Minemoto, K. (2011). Cognitive adaptations for gathering-related navigation in humans. *Evolution and Human Behavior*, 32(1), 1–12. DOI:10.1016/j.evolhumbehav.2010.07.003

Lambert, J. E. (1998). Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evolutionary Anthropology: Issues, News, and Reviews*, 7(1), 8–20. DOI:10.1002/(SICI)1520-6505(1998)7:1<8::AID-EVAN3>3.0.CO;2-C

Landler, L., Ruxton, G. D., & Pascal Malkemper, E. (2018). Circular data in biology: advice for effectively implementing statistical procedures. *Behavioral Ecology and Sociobiology*, 72(8), 128–135. DOI:10.1007/s00265-018-2538-y

LaPoint, S., Gallery, P., Wikelski, M., & Kays, R. (2013). Animal behavior, cost-based corridor models, and real corridors. *Landscape Ecology*, 28(8), 1615–1630. DOI:10.1007/s10980-013-9910-0

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Fission-fusion social systems as a strategy for coping with ecological constraints: a primate case. *Evolutionary Ecology*, 21(5), 613–634. DOI:10.1007/s10682-006-9141-9

Leroy, E. M., Epelboin, A., Mondonge, V., Pourrut, X., Gonzalez, J. P., Muyembe-Tamfum, J. J., & Formenty, P. (2009). Human ebola outbreak resulting from direct

exposure to fruit bats in Luebo, Democratic Republic of Congo, 2007. *Vector-Borne and Zoonotic Diseases*, 9(6), 723–728. DOI:10.1089/vbz.2008.0167

Lewis, J. (2002). *Forest hunter-gatherers and their world: a study of the Mbendjele Yaka Pygmies of Congo-Brazzaville and their secular and religious activities and representations*. University of London.

Liedvogel, M., Åkesson, S., & Bensch, S. (2011). The genetics of migration on the move. *Trends in Ecology and Evolution*, 26(11), 561–569. DOI:10.1016/j.tree.2011.07.009

Logan, C. J., Avin, S., Boogert, N., Buskell, A., Cross, F. R., Currie, A., … Montgomery, S. H. (2018). Beyond brain size: uncovering the neural correlates of behavioral and cognitive specialization. *Comparative Cognition and Behavior Reviews*, 13, 55–90. DOI:10.3819/CCBR.2018.130008

Lohmann, K. J., Lohmann, C. M. F., Ehrhart, L. M., Bagley, D. A., & Swing, T. (2004). Geomagnetic map used in sea-turtle navigation. *Nature*, 428(6986), 909–910. DOI:10.1038/428909a

Lovejoy, C. O. (2009). Reexamining human origins in light of Ardipithecus ramidus. *Science*, 326(5949), 74–78. DOI:10.1126/science.1175834

Lührs, M. L., Dammhahn, M., Kappeler, P. M., & Fichtel, C. (2009). Spatial memory in the grey mouse lemur (*Microcebus murinus*). *Animal Cognition*, 12(4), 599–609. DOI:10.1007/s10071-009-0219-y

Lundberg, J., & Moberg, F. (2003). Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems*, 6(1), 87–98. DOI:10.1007/s10021-002-0150-4

MacLean, E. L., Barrickman, N. L., Johnson, E. M., & Wall, C. E. (2009). Sociality, ecology, and relative brain size in lemurs. *Journal of Human Evolution*, 56(5), 471–478. DOI:10.1016/j.jhevol.2008.12.005

Magnusson, K. R., Hauck, L., Jeffrey, B. M., Elias, V., Humphrey, A., Nath, R., … Bermudez, L. E. (2015). Relationships between diet-related changes in the gut microbiome and cognitive flexibility. *Neuroscience*, 300, 128–140. DOI:10.1016/j.neuroscience.2015.05.016

Majid, A., Bowerman, M., Kita, S., Haun, D. B. M., & Levinson, S. C. (2004). Can language restructure cognition? The case for space. *Trends in Cognitive Sciences*, 8(3), 108–114. DOI:10.1016/j.tics.2004.01.003

Mann, R. P., Armstrong, C., Meade, J., Freeman, R., Biro, D., & Guilford, T. (2014). Landscape complexity influences route memory formation in navigating pigeons. *Biology Letters*, 10(1), 20130885. DOI:10.1098/rsbl.2013.0885

Manrique, H. M., Völter, C. J., & Call, J. (2013). Repeated innovation in great apes. *Animal Behaviour*, 85(1), 195–202. DOI:10.1016/j.anbehav.2012.10.026

Marino, L., Sudheimer, K. D., Pabst, D. A., McLellan, W. A., Filsoof, D., & Johnson, J. I. (2002). Neuroanatomy of the common dolphin (*Delphinus delphis*) as revealed by magnetic resonance imaging (MRI). *Anatomical Record*, 268(4), 411–429.

DOI:10.1002/ar.10181

Marks, J. S., & Redmond, R. L. (1994). Migration of bristle-thighed curlews on Laysan island: timing, behavior and estimated flight range. *The Condor*, 96(2), 316–330. DOI:10.2307/1369317

Martin-Ordas, G., Haun, D. B. M., Colmenares, F., & Call, J. (2010). Keeping track of time: Evidence for episodic-like memory in great apes. *Animal Cognition*, 13(2), 331–340. DOI:10.1007/s10071-009-0282-4

Martin, R. D. (1981). Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature*, 293(5827), 57–60. DOI:10.1038/293057a0

Martinez-Ramos, M., Alvarez-Buylla, E., Sarukhan, J., & Piñero, D. (1998). Treefall age determination and gap dynamics in a tropical forest. *Journal of Ecology*, 76(3), 700–716.

Mauck, B., Gläser, N., Schlosser, W., & Dehnhardt, G. (2008). Harbour seals (*Phoca vitulina*) can steer by the stars. *Animal Cognition*, 11(4), 715–718. DOI:10.1007/s10071-008-0156-1

McLean, K. A., Trainor, A. M., Asner, G. P., Crofoot, M. C., Hopkins, M. E., Campbell, C. J., … Jansen, P. A. (2016). Movement patterns of three arboreal primates in a Neotropical moist forest explained by LiDAR-estimated canopy structure. *Landscape Ecology*, 31(8), 1849–1862. DOI:10.1007/s10980-016-0367-9

McNaughton, B. L., Battaglia, F. P., Jensen, O., Moser, E. I., & Moser, M.-B. (2006). Path integration and the neural basis of the "cognitive map." *Nature Reviews Neuroscience*, 7(8), 663–678. DOI:10.1038/nrn1932

Meekan, M. G., Duarte, C. M., Fernández-Gracia, J., Thums, M., Sequeira, A. M. M., Harcourt, R., & Eguíluz, V. M. (2017). The ecology of human mobility. *Trends in Ecology and Evolution*, 32(3), 198–210. DOI:10.1016/j.tree.2016.12.006

Meier, E. S., Kienast, F., Pearman, P. B., Svenning, J. C., Thuiller, W., Araújo, M. B., … Zimmermann, N. E. (2010). Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography*, 33(6), 1038–1048. DOI:10.1111/j.1600-0587.2010.06229.x

Mercado III, E., & DeLong, C. M. (2010). Dolphin cognition: representations and processes in memory and perception. *International Journal of Comparative Psychology*, 23, 344–378.

Meredith, R. W., Janečka, J. E., Gatesy, J., Ryder, O. A., Fisher, C. A., Teeling, E. C., … Murphy, W. J. (2011). Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science*, 334(6055), 521–524. DOI:10.1126/science.1211028

Mery, F., & Kawecki, T. J. (2003). A fitness cost of learning ability in *Drosophila melanogaster*. *Proceedings of the Royal Society B: Biological Sciences*, 270(1532), 2465–2469. DOI:10.1098/rspb.2003.2548

Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *The American Anthropologist*, 83, 534–548.

Milton, K. (1984). The role of food-processing factors in primate food choice. In P. Rodman & J. Cant (Eds.), *Adaptations for foraging in nonhuman primtes* (pp. 249–279). New York, US: Columbia University Press.

Milton, K., & May, M. L. (1976). Body weight, diet and home range area in primates. *Nature*, 259(5543), 459–462. DOI:10.1038/259459a0

Mittelstaedt, H., & Mittelstaedt, M.-L. (1982). Homing by path integration. In *Avian Navigation* (pp. 290–297). DOI:10.1007/978-3-642-68616-0_29

Mocanu, D., Baronchelli, A., Perra, N., Gonçalves, B., Zhang, Q., & Vespignani, A. (2013). The twitter of babel: mapping world languages through microblogging platforms. *PLoS ONE*, 8(4), e61981. DOI:10.1371/journal.pone.0061981

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., … Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2289–2301. DOI:10.1098/rstb.2010.0082

Morand-Ferron, J. (2017). Why learn? The adaptive value of associative learning in wild populations. *Current Opinion in Behavioral Sciences*, 16, 73–79. DOI:10.1016/j.cobeha.2017.03.008

Moser, E. I., Kropff, E., & Moser, M. B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annual Review of Neuroscience*, 31(1), 69–89. DOI:10.1146/annurev.neuro.31.061307.090723

Moser, M. B., Rowland, D. C., & Moser, E. I. (2015). Place cells, grid cells, and memory. *Cold Spring Harbor Perspectives in Biology*, 7(2), a021808. DOI:10.1101/cshperspect.a021808

Mueller, T., Olson, K. A., Dressler, G., Leimgruber, P., Fuller, T. K., Nicolson, C., … Fagan, W. F. (2011). How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Global Ecology and Biogeography*, 20(5), 683–694. DOI:10.1111/j.1466-8238.2010.00638.x

Myneni, R. B., Maggion, S., Iaquinta, J., Privette, J. L., Gobron, N., Pinty, B., … Williams, D. L. (1995). Optical remote sensing of vegetation: modeling, caveats, and algorithms. *Remote Sensing of Environment*, 51(1), 169–188. DOI:10.1016/0034-4257(94)00073-V

Naik, H., Bastien, R., Navab, N., & Couzin, I. D. (2020). Animals in virtual environments. *IEEE Transactions on Visualization and Computer Graphics*. DOI:10.1109/TVCG.2020.2973063

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, 105(49), 19052–19059. DOI:10.1073/pnas.0800375105

Navarrete, A., Van Schaik, C. P., & Isler, K. (2011). Energetics and the evolution of human brain size. *Nature*, 480(7375), 91–93. DOI:10.1038/nature10629

Nelson, A., Reuter, H. I., & Gessler, P. (2009). DEM production methods and sources. In M. Busse, C. Giardina, D. Morris, & D. Page-Dumroese (Eds.), *Developments in soil science* (Vol. 33, pp. 65–85). DOI:10.1016/S0166-2481(08)00003-2

Neumann, C., & Zuberbühler, K. (2016). Vocal correlates of individual sooty mangabey travel speed and direction. *PeerJ*, 4, e2298. DOI:10.7717/peerj.2298

Nevo, O., & Heymann, E. W. (2015). Led by the nose: olfaction in primate feeding ecology. *Evolutionary Anthropology: Issues, News and Reviews*, 24(4), 137–148. DOI:10.1002/evan.21458

Newmark, W. D., & Rickart, E. A. (2012). High-use movement pathways and habitat selection by ungulates. *Mammalian Biology*, 77(4), 293–298. DOI:10.1016/j.mambio.2012.03.007

Nöremark, M., Håkansson, N., Lewerin, S. S., Lindberg, A., & Jonsson, A. (2011). Network analysis of cattle and pig movements in Sweden: measures relevant for disease control and risk based surveillance. *Preventive Veterinary Medicine*, 99(2–4), 78–90. DOI:10.1016/j.prevetmed.2010.12.009

Noren, S. R., Williams, T. M., Pabst, D. A., McLellan, W. A., & Dearolf, J. L. (2001). The development of diving in marine endotherms: preparing the skeletal muscles of dolphins, penguins, and seals for activity during submergence. *Journal of Comparative Physiology*, 171(2), 127–134. DOI:10.1007/s003600000161

Normand, E., & Boesch, C. (2009). Sophisticated Euclidean maps in forest chimpanzees. *Animal Behaviour*, 77(5), 1195–1201. DOI:10.1016/j.anbehav.2009.01.025

Noser, R., & Byrne, R. W. (2007a). Mental maps in chacma baboons (*Papio ursinus*): using inter-group encounters as a natural experiment. *Animal Cognition*, 10(3), 331–340. DOI:10.1007/s10071-006-0068-x

Noser, R., & Byrne, R. W. (2007b). Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, *Papio ursinus*. *Animal Behaviour*, 73(2), 257–266. DOI:10.1016/j.anbehav.2006.04.012

Noser, R., & Byrne, R. W. (2014). Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons. *American Journal of Primatology*, 76(5), 399–409. DOI:10.1002/ajp.22181

Noser, R., & Byrne, R. W. (2015). Wild chacma baboons (*Papio ursinus*) remember single foraging episodes. *Animal Cognition*, 18(4), 921–929. DOI:10.1007/s10071-015-0862-4

O'Keefe, J., & Nadel, L. (1978). The Hippocampus as a cognitive map. In *The hippocampus as a cognitive map*. Oxford University Press.

Oleksiak, A., Postma, A., van der Ham, I. J. M., Klink, P. C., & van Wezel, R. J. A. (2011). A review of lateralization of spatial functioning in nonhuman primates. *Brain Research Reviews*, 67(1–2), 56–72. DOI:10.1016/j.brainresrev.2010.11.002

Osorio, D., Smith, A. C., Vorobyev, M., & Buchanan-Smith, H. M. (2004). Detection of fruit and the selection of primate visual pigments for color vision. *The American Naturalist*, 164(6), 696–708. DOI:10.1086/425332

Osorio, D., & Vorobyev, M. (1996). Colour vision as an adaptation to frugivory in primates. *Proceedings of the Royal Society B: Biological Sciences*, 263(1370), 593–599. DOI:10.1098/rspb.1996.0089

Ostro, L. E. T., Silver, S. C., Koontz, F. W., Young, T. P., & Horwich, R. H. (1999). Ranging behavior of translocated and established groups of black howler monkeys *Alouatta pigra* in Belize, Central America. *Biological Conservation*, 87(2), 181–190.

Palacios-Romo, T. M., Castellanos, F., & Ramos-Fernandez, G. (2019). Uncovering the decision rules behind collective foraging in spider monkeys. *Animal Behaviour*, 149, 121–133. DOI:10.1016/j.anbehav.2019.01.011

Pavelka, M. S. M., & Knopff, K. H. (2004). Diet and activity in black howler monkeys (*Alouatta pigra*) in Southern Belize: does degree of frugivory influence activity level? *Primates*, 45(2), 105–111. DOI:10.1007/s10329-003-0072-6

Pebesma, E., Bivand, R., Racine, E., Sumner, M., Cook, I., Keitt, T., … Lin Pedersen, T. (2019). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, 10(1), 439–446. DOI:10.32614/RJ-2018-009

Perdeck, A. C. (1958). Two types of orientation in migrating starlings, *Sturnus yulgaris* L., and chaffinches, *Fringilla coelebs* L., as revealed by displacement experiments. *Ardea*, 55, 1–2.

Pereira, T. S. (2008). *Ecologia cognitiva e forrageamento de* Alouatta guariba clamitans *Cabrera, 1940: os bugios-ruivos possuem mapas mentais?* Pontifícia Universidade Católica do Rio Grande do Sul.

Peters, W., Hebblewhite, M., Mysterud, A., Spitz, D., Focardi, S., Urbano, F., … Cagnacci, F. (2017). Migration in geographic and ecological space by a large herbivore. *Ecological Monographs*, 87(2), 297–320. DOI:10.1002/ecm.1250

Petit, O., & Bon, R. (2010). Decision-making processes: the case of collective movements. *Behavioural Processes*, 84, 635–647. DOI:10.1016/j.beproc.2010.04.009

Piéron, H. (1904). Du role du sens musculaire dans l'orientation de quelques espèces de fourmis. *Bulletin Inst. General Psychologique*, 4, 168–186.

Plaçais, P.-Y., & Preat, T. (2013). To favor survival under food shortage, the brain disables costly memory. *Science*, 339(6118), 440–442. DOI:10.1126/science.1226018

Pladevall, J., Mendes, N., Riba, D., Llorente, M., & Amici, F. (2020). No evidence of what-where-when memory in great apes (*Pan troglodytes*, *Pan paniscus*, *Pongo abelii*, and *Gorilla gorilla*). *Journal of Comparative Psychology*. DOI:10.1037/com0000215

Plante, S., Colchero, F., & Calmé, S. (2014). Foraging strategy of a neotropical primate: how intrinsic and extrinsic factors influence destination and residence time. *Journal of Animal Ecology*, 83(1), 116–125. DOI:10.1111/1365-2656.12119@10.1111/(ISSN)1365-2656.MOVEMENTECOLOGY

Poindexter, S. A. (2017). *Navigating the night: spatial cognition, locomotor and ranging behaviour in Nycticebus species* (Oxford Brookes University). DOI:10.24384/RNPT-3335

Porter, L.M., Garber, P. A., Boesch, C., & Janmaat, K. M. R. (2020). Using GIS to examine long-term foraging strategies in tamarins and chimpanzees. In C. Shaffer, F. Dolins, J. Hickey, N. Nibbelink, & L. Porter (Eds.), *GPS and GIS for primatologists: a practical guide to spatial analysis*. Cambridge, UK: Cambridge University Press.

Porter, Leila M., & Garber, P. A. (2013). Foraging and spatial memory in wild Weddell's saddleback tamarins (*Saguinus fuscicollis weddelli*) when moving between distant and out-of-sight goals. *International Journal of Primatology*, 34(1), 30–48. DOI:10.1007/s10764-012-9644-x

Potts, J. R., Börger, L., Scantlebury, D. M., Bennett, N. C., Alagaili, A., & Wilson, R. P. (2018). Finding turning-points in ultra-high-resolution animal movement data. *Methods in Ecology and Evolution*, 9(10), 2091–2101. DOI:10.1111/2041-210X.13056

Poucet, B. (1993). Spatial cognitive maps in animals: new hypotheses on their structure and neural mechanisms. *Psychological Review*, 100(2), 163–182.

Powell, L. E., Isler, K., & Barton, R. A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society B: Biological Sciences*, 284(1865), 20171765. DOI:10.1098/rspb.2017.1765

Presotto, A. (2009). *Primates cognitive maps: analysis of movements and routes of Cebus nigritus based on geographic information system*. University of São Paulo.

Presotto, A., & Izar, P. (2010). Spatial reference of black capuchin monkeys in Brazilian Atlantic Forest: egocentric or allocentric? *Animal Behaviour*, 80(1), 125–132. DOI:10.1016/j.anbehav.2010.04.009

Presotto, A., Verderane, M. P., Biondi, L., Mendonça-Furtado, O., Spagnoletti, N., Madden, M., & Izar, P. (2018). Intersection as key locations for bearded capuchin monkeys (*Sapajus libidinosus*) traveling within a route network. *Animal Cognition*, 21(3), 393–405. DOI:10.1007/s10071-018-1176-0

Presotto, Andrea, Fayrer-Hosken, R., Curry, C., & Madden, M. (2019). Spatial mapping shows that some African elephants use cognitive maps to navigate the core but not the periphery of their home ranges. *Animal Cognition*, 22(2), 251–263. DOI:10.1007/s10071-019-01242-9

Proulx, M. J., Todorov, O. S., Aiken, A. T., & de Sousa, A. A. (2016). Where am I? Who am I? The relation between spatial cognition, social cognition and individual differences in the built environment. *Frontiers in Psychology*, 7(64). DOI:10.3389/fpsyg.2016.00064

Quaglietta, L., & Porto, M. (2019). SiMRiv: an R package for mechanistic simulation of individual, spatially-explicit multistate movements in rivers, heterogeneous and homogeneous spaces incorporating landscape bias. *Movement Ecology*, 7(1), 1–11. DOI:10.1186/s40462-019-0154-8

Raby, C. R., Alexis, D. M., Dickinson, A., & Clayton, N. S. (2007). Planning for the future by western scrub-jays. *Nature*, 445(7130), 919. DOI:10.1038/nature05575

Ramsier, M. A., Cunningham, A. J., Patiño, M. R., Glander, K. E., & Dominy, N. J. (2019). Audiograms of howling monkeys: are extreme loud calls the result of runaway selection? *BioRxiv*, 539023. DOI:10.1101/539023

Ranc, N., Cagnacci, F., & Moorcroft, P. (2020). Memory drives the formation of animal home ranges: evidence from a reintroduction. *BioArxiv*.

Rangel-Negrín, A., Coyohua-Fuentes, A., Canales-Espinosa, D., & Dias, P. A. D. (2018). The influence of leaf consumption on time allocation in black howler monkeys (*Alouatta pigra*). *Folia Primatologica*, 89(2), 111–122. DOI:10.1159/000486414

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, 99(7), 4436–4441. DOI:10.1073/pnas.062041299

Reed, K. E. (1997). Early hominid evolution and ecological change through the African Plio-Pleistocene. *Journal of Human Evolution*, 32(2–3), 289–322. DOI:10.1006/jhev.1996.0106

Reich, P. B. (1995). Phenology of tropical forests: patterns, causes, and consequences. *Canadian Journal of Botany*, 73(2), 164–174. DOI:10.1139/b95-020

Reidenberg, J. S. (2007). Anatomical adaptations of aquatic mammals. *Anatomical Record*, 290(6), 507–513. DOI:10.1002/ar.20541

Reppert, S. M., & de Roode, J. C. (2018). Demystifying monarch butterfly migration. *Current Biology*, 28(17), R1009–R1022. DOI:10.1016/j.cub.2018.02.067

Reyna-Hurtado, R., Teichroeb, J. A., Bonnell, T. R., Hernández-Sarabia, R. U., Vickers, S. M., Serio-Silva, J. C., … Chapman, C. A. (2018). Primates adjust movement strategies due to changing food availability. *Behavioral Ecology*, 29(2), 368–376. DOI:10.1093/beheco/arx176

Righini, N., Garber, P. A., & Rothman, J. M. (2017). The effects of plant nutritional chemistry on food selection of Mexican black howler monkeys (*Alouatta pigra*): the role of lipids. *American Journal of Primatology*, 79(4), 1–15. DOI:10.1002/ajp.22524

Riley, J. R., Greggers, U., Smith, A. D., Reynolds, D. R., & Menzel, R. (2005). The flight paths of honeybees recruited by the waggle dance. *Nature*, 435(7039), 205–207. DOI:10.1038/nature03526

Riotte-Lambert, L., & Matthiopoulos, J. (2020). Environmental predictability as a cause and consequence of animal movement. *Trends in Ecology and Evolution*, 35(2), 163–174. DOI:10.1016/j.tree.2019.09.009

Robbins, M. M., & McNeilage, A. (2003). Home range and frugivory patterns of mountain gorillas in Bwindi Impenetrable National Park, Uganda. *International Journal of Primatology*, 24(3), 467–491. DOI:10.1023/A:1023741328338

Rogers, M. E., Abernethy, K., Bermejo, M., Cipolletta, C., Doran, D., Mcfarland, K., … Tutin, C. E. G. (2004). Western gorilla diet: a synthesis from six sites. *American Journal of Primatology*, 64(2), 173–192. DOI:10.1002/ajp.20071

Rome, L. C., & Lindstedt, S. L. (1998). The quest for speed: muscles built for high-frequency contractions. *Physiology*, 13(6), 261–268. DOI:10.1152/physiologyonline.1998.13.6.261

Rosati, A. G. (2017). Foraging Cognition: Reviving the Ecological Intelligence Hypothesis. *Trends in Cognitive Sciences*, 21(9), 691–702. DOI:10.1016/j.tics.2017.05.011

Rosenbaum, R. S., Köhler, S., Schacter, D. L., Moscovitch, M., Westmacott, R., Black, S. E., … Tulving, E. (2005). The case of K.C.: contributions of a memory-impaired person to memory theory. *Neuropsychologia*, 43(7), 989–1021. DOI:10.1016/J.NEUROPSYCHOLOGIA.2004.10.007

Rosenberg, K., & Trevathan, W. (1995). Bipedalism and human birth: the obstetrical dilemma revisited. *Evolutionary Anthropology: Issues, News, and Reviews*, 4(5), 161–168. DOI:10.1002/evan.1360040506

Roy, D. P., Wulder, M. A., Loveland, T. R., C.E., W., Allen, R. G., Anderson, M. C., … Zhu, Z. (2014). Landsat-8: science and product vision for terrestrial global change research. *Remote Sensing of Environment*, 145, 154–172. DOI:10.1016/j.rse.2014.02.001

Rubenstein, D. R., & Hobson, K. A. (2004). From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution*, 19(5), 256–263. DOI:10.1016/j.tree.2004.03.017

Ruxton, G. D. (2017). Testing for departure from uniformity and estimating mean direction for circular data. *Biology Letters*, 13(1), 20160756. DOI:10.1098/rsbl.2016.0756

Salmi, R., Presotto, A., Scarry, C. J., Hawman, P., & Doran-Sheehy, D. M. (2020). Spatial cognition in western gorillas (*Gorilla gorilla*): an analysis of distance, linearity, and speed of travel routes. *Animal Cognition*, 1–13. DOI:10.1007/s10071-020-01358-3

Sanders, H., Rennó-Costa, C., Idiart, M., & Lisman, J. (2015). Grid cells and place cells: an integrated view of their navigational and memory function. *Trends in Neurosciences*, 38(12), 763–775. DOI:10.1016/j.tins.2015.10.004

Sasaki, T., & Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications*, 8, 15049. DOI:10.1038/ncomms15049

Saunders, D. A. (1980). Food and movements of the short-billed form of the white-tailed black cockatoo. *Wildlife Research*, 7(2), 257–269. DOI:10.1071/WR9800257

Sauther, M. L., Sussman, R. W., & Gould, L. (1999). The socioecology of the ringtailed lemur: thirty-five years of research. *Evolutionary Anthropology: Issues, News, and Reviews*, 8(4), 120–132. DOI:10.1002/(SICI)1520-6505(1999)8:4<120::AID-EVAN3>3.0.CO;2-O

Sawyer, H., Merkle, J. A., Middleton, A. D., Dwinnell, S. P. H., & Monteith, K. L. (2018). Migratory plasticity is not ubiquitous among large herbivores. *Journal of Animal Ecology*, 88(3), 450–460. DOI:10.1111/1365-2656.12926

Sayol, F., Maspons, J., Lapiedra, O., Iwaniuk, A. N., Székely, T., & Sol, D. (2016). Environmental variation and the evolution of large brains in birds. *Nature Communications*, 7(1), 1–8. DOI:10.1038/ncomms13971

Schacter, D. L., & Addis, D. R. (2007). The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1481), 773–786. DOI:10.1098/rstb.2007.2087

Schaeffer, P. J., & Lindstedt, S. L. (2013). How animals move: comparative lessons on animal locomotion. *Comprehensive Physiology*, 3(1), 289–314. DOI:10.1002/cphy.c110059

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee alarm call production meets key criteria for intentionality. *PLoS ONE*, 8(10). DOI:10.1371/journal.pone.0076674

Schieber, T. A., Carpi, L., Díaz-Guilera, A., Pardalos, P. M., Masoller, C., & Ravetti, M. G. (2017). Quantification of network structural dissimilarities. *Nature Communications*, 8(1), 1–10. DOI:10.1038/ncomms13928

Schmidt, K. A., Dall, S. R. X., & van Gils, J. A. (2010). The ecology of information: an overview on the ecological significance of making informed decisions. *Oikos*, 119(2), 304–316. DOI:10.1111/j.1600-0706.2009.17573.x

Schoener, T. W. (1971). Theory of feeding strategies. *Annual Reviews Ecological Systems*, 2, 369–404.

Schön, M. A. (1971). The anatomy of the resonating mechanism in howling monkeys. *Folia Primatologica*, 15(1–2), 117–132. DOI:10.1159/000155371

Schreier, A. L., & Grove, M. (2014). Recurrent patterning in the daily foraging routes of hamadryas baboons (*Papio hamadryas*): spatial memory in large-scale versus small-scale space. *American Journal of Primatology*, 76(5), 421–435. DOI:10.1002/ajp.22192

Seidel, D. P., Dougherty, E., Carlson, C., & Getz, W. M. (2018). Ecological metrics and methods for GPS movement data. *International Journal of Geographical Information Science*, 32(11). DOI:10.1080/13658816.2018.1498097

Seymour, R. S., Bosiocic, V., & Snelling, E. P. (2016). Fossil skulls reveal that blood flow rate to the brain increased faster than brain volume during human evolution. *Royal Society Open Science*, 3(8). DOI:10.1098/rsos.160305

Shepard, E. L. C., Wilson, R. P., Gareth Rees, W., Grundy, E., Lambertucci, S. A., & Vosper, S. B. (2013). Energy landscapes shape animal movement ecology. *The American Naturalist*, 182(3), 298–312. DOI:10.1086/671257

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (2nd ed.). New York, US: Oxford University Press.

Sigg, H., & Stolba, A. (1981). Home range and daily march in a Hamadryas baboon troop. *Folia Primatologica*, 36(1–2), 40–75. DOI:10.1159/000156008

Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, 4(2), 367–387. DOI:10.1111/j.1752-4571.2010.00166.x

Sih, A., Spiegel, O., Godfrey, S., Leu, S., & Bull, C. M. (2018). Integrating social networks, animal personalities, movement ecology and parasites: a framework with examples from a lizard. *Animal Behaviour*, 136, 195–205. DOI:10.1016/j.anbehav.2017.09.008

Silver, S. C., Ostro, L. E. T., Yeager, C. P., & Horwich, R. (1998). Feeding ecology of the black howler monkey (*Alouatta pigra*) in Northern Belize. *American Journal of Primatology*, 45(3), 263–279. DOI:10.1002/(SICI)1098-2345(1998)45:3<263::AID-AJP3>3.0.CO;2-U

Singh, N. J., & Ericsson, G. (2014). Changing motivations during migration: linking movement speed to reproductive status in a migratory large mammal. *Biology Letters*, 10(6). DOI:10.1098/rsbl.2014.0379

Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, 85(5), 1004–1011. DOI:10.1016/j.anbehav.2012.12.031

Soh, H., Lim, S., Zhang, T., Fu, X., Lee, G. K. K., Hung, T. G. G., … Wong, L. (2010). Weighted complex network analysis of travel routes on the Singapore public transportation system. *Physica A: Statistical Mechanics and Its Applications*, 389(24), 5852–5863. DOI:10.1016/j.physa.2010.08.015

Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters*, 5(1), 130–133. DOI:10.1098/rsbl.2008.0621

Sol, D., Bacher, S., Reader, S. M., & Lefebvre, L. (2008). Brain size predicts the success of mammal species introduced into novel environments. *The American Naturalist*, 172, 63. DOI:10.1086/588304

Sol, D., Timmermans, S., & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour*, 63(3), 495–502. DOI:10.1006/anbe.2001.1953

Somveille, M., Firth, J. A., Aplin, L. M., Farine, D. R., Sheldon, B. C., & Thompson, R. N. (2018). Movement and conformity interact to establish local behavioural traditions in animal populations. *PLoS Computational Biology*, 14(12), e1006647. DOI:10.1371/journal.pcbi.1006647

Sperber, A. L., Kappeler, P. M., & Fichtel, C. (2019). Should I stay or should I go? Individual movement decisions during group departures in red-fronted lemurs.

Royal Society Open Science, 6(3), 180991. DOI:10.1098/rsos.180991

Spiegel, O., & Crofoot, M. C. (2016). The feedback between where we go and what we know — information shapes movement, but movement also impacts information acquisition. *Current Opinion in Behavioral Sciences*, 12, 90–96. DOI:10.1016/j.cobeha.2016.09.009

Spiegel, O., Harel, R., Getz, W. M., & Nathan, R. (2013). Mixed strategies of griffon vultures' (*Gyps fulvus*) response to food deprivation lead to a hump-shaped movement pattern. *Movement Ecology*, 1(1), 1–5. DOI:10.1186/2051-3933-1-5

Spiegel, O., Leu, S. T., Sih, A., Godfrey, S. S., & Bull, C. M. (2015). When the going gets tough: behavioural type-dependent space use in the sleepy lizard changes as the season dries. *Proceedings of the Royal Society B: Biological Sciences*, 282(1819), 20151768. DOI:10.1098/rspb.2015.1768

Steiper, M. E., & Seiffert, E. R. (2012). Evidence for a convergent slowdown in primate molecular rates and its implications for the timing of early primate evolution. *Proceedings of the National Academy of Sciences*, 109(16), 6006–6011. DOI:10.1073/pnas.1119506109

Strandburg-Peshkin, A., Farine, D. R., Papageorgiou, D., & Crofoot, M. C. (2018). Inferring influence and leadership in moving animal groups. *Proceedings of the Royal Society B: Biological Sciences*, 373(1746), 20170006. DOI:10.1098/rstb.2017.0006

Suarez, S. A. (2003). *Spatio-temporal foraging skills of white-bellied spider monkeys (Ateles belzebuth belzebuth) in the Yasuni National Park, Ecuador.* (State University of New York at Stony Brook). State University of New York at Stony Brook.

Suarez, S. A. (2014). Ecological factors predictive of wild spider monkey (*Ateles belzebuth*) foraging decisions in Yasuní, Ecuador. *American Journal of Primatology*, 76(12), 1185–1195. DOI:10.1002/ajp.22303

Suarez, S. A., Karro, J., Kiper, J., Farler, D., Mcelroy, B., Rogers, B. C., … Young, T. (2014). A comparison of computer-generated and naturally occurring foraging patterns in route-network-constrained spider monkeys. *American Journal of Primatology*, 76(5), 460–471. DOI:10.1002/ajp.22222

Suddendorf, T. (2013). Mental time travel: continuities and discontinuities. *Trends in Cognitive Sciences*, 17(4), 151–152. DOI:10.1016/j.tics.2013.01.011

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., … Aureli, F. (2011). Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos*, 120(11), 1608–1617. DOI:10.1111/j.1600-0706.2011.19685.x

Sussman, R. W. (1991). Primate origins and the evolution of angiosperms. *American Journal of Primatology*, 23(4), 209–223. DOI:10.1002/ajp.1350230402

Sussman, R. W., Tab Rasmussen, D., & Raven, P. H. (2013). Rethinking primate origins again. *American Journal of Primatology*, 75(2), 95–106. DOI:10.1002/ajp.22096

Taylor, L. A., Portugal, S. J., & Biro, D. (2017). Homing pigeons (*Columba livia*) modulate wingbeat characteristics as a function of route familiarity. *Journal of Experimental Biology*, 220(16), 2908–2915. DOI:10.1242/jeb.154039

Taylor, L. A., Vollrath, F., Lambert, B., Lunn, D., Douglas-Hamilton, I., & Wittemyer, G. (2020). Movement reveals reproductive tactics in male elephants. *Journal of Animal Ecology*, 89(1), 57–67. DOI:10.1111/1365-2656.13035

Tello-Ramos, M. C., Branch, C. L., Kozlovsky, D. Y., Pitera, A. M., & Pravosudov, V. V. (2019). Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the question. *Animal Behaviour*, 147. DOI:10.1016/j.anbehav.2018.02.019

Templer, V. L., & Hampton, R. R. (2013). Episodic memory in nonhuman animals. *Current Biology*, 23(17), R801–R806. DOI:10.1016/j.cub.2013.07.016

Thorpe, S. K. S., Crompton, R. H., & Alexander, R. M. (2007). Orangutans use compliant branches to lower the energetic cost of locomotion. *Biology Letters*, 3(3), 253–256. DOI:10.1098/rsbl.2007.0049

Thums, M., Fernández-Gracia, J., Sequeira, A. M. M., Eguíluz, V. M., Duarte, C. M., & Meekan, M. G. (2018). How big data fast tracked human mobility research and the lessons for animal movement ecology. *Frontiers in Marine Science*, 5(FEB), 21. DOI:10.3389/fmars.2018.00021

Tian, F., Fensholt, R., Verbesselt, J., Grogan, K., Horion, S., & Wang, Y. (2015). Evaluating temporal consistency of long-term global NDVI datasets for trend analysis. *Remote Sensing of Environment*, 163, 326–340. DOI:10.1016/j.rse.2015.03.031

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, 55(4), 189–208.

Tomasello, M., & Call, J. (1997). *Primate cognition* (M. Tomasello & J. Call, Eds.). New York, US: Oxford University Press.

Trapanese, C., Meunier, H., & Masi, S. (2019). What, where and when: spatial foraging decisions in primates. *Biological Reviews*, 94(2), 483–502. DOI:10.1111/brv.12462

Tucker, C. J. (1979). *Red and photographic infrared linear combinations for monitoring vegetation*.

Tucker, C. J., Pinzon, J. E., Brown, M. E., Slayback, D. A., Pak, E. W., Mahoney, R., … El Saleous, N. (2005). An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. *International Journal of Remote Sensing*, 26(20), 4485–4498. DOI:10.1080/01431160500168686

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., … Mueller, T. (2018). Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science*, 359(6374), 466–469. DOI:10.1126/science.aam9712

Tujague, M. P., & Janson, C. H. (2018). Foraging cognition in Neotropical primates: integrating studies from the wild and from captivity. In Martin M. Kowalewski & L. I. Oklaender (Eds.), *Primatology in Argentina*. Buenos Aires: SAREM.

Urbani, B. (2009). *Spatial mapping in wild white faced capuchin monkeys (Cebus Capucinus)*. University of Illinois at Urbana-Champaign.

Valero, A., & Byrne, R. W. (2007). Spider monkey ranging patterns in Mexican subtropical forest: do travel routes reflect planning? *Animal Cognition*, 10(3), 305–315. DOI:10.1007/s10071-006-0066-z

Van Belle, S., & Bicca-Marques, J. C. (2015). Insights into reproductive strategies and sexual selection in howler monkeys. In M.M. Kowalewski, P. A. Garber, L. Cortes-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behavior, ecology, and conservation* (pp. 57–84). DOI:10.1007/978-1-4939-1960-4_3

Van Belle, S., & Estrada, A. (2006). Demographic features of *Alouatta pigra* populations in extensive and fragmented forests. In A. Estrada, P. A. Garber, M. S. M. Pavelka, & L. Luecke (Eds.), *New perspectives in the study of mesoamerican primates* (pp. 121–142). DOI:10.1007/0-387-25872-8_6

Van Belle, S., & Estrada, A. (2019). The influence of loud calls on intergroup spacing mechanism in black howler monkeys (*Alouatta pigra*). *International Journal of Primatology*.

Van Belle, S., Estrada, A., & Garber, P. A. (2013a). Collective group movement and leadership in wild black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology*, 67(1), 31–41. DOI:10.1007/s00265-012-1421-5

Van Belle, S., Estrada, A., & Garber, P. A. (2013b). Spatial and diurnal distribution of loud calling in black howlers (*Alouatta pigra*). *International Journal of Primatology*, 34(6), 1209–1224. DOI:10.1007/s10764-013-9734-4

Van Belle, S., Estrada, A., Strier, K. B., & Di Fiore, A. (2012). Genetic structure and kinship patterns in a population of black howler monkeys, *Alouatta pigra*, at Palenque National Park, Mexico. *American Journal of Primatology*, 74(10), 948–957. DOI:10.1002/ajp.22047

Van Belle, S., Estrada, A., Ziegler, T. E., & Strier, K. B. (2009). Sexual behavior across ovarian cycles in wild black howler monkeys (*Alouatta pigra*): male mate guarding and female mate choice. *American Journal of Primatology*, 71(2), 153–164. DOI:10.1002/ajp.20635

Van Belle, S., Garber, P. A., Estrada, A., & Di Fiore, A. (2014). Social and genetic factors mediating male participation in collective group defence in black howler monkeys. *Animal Behaviour*, 98, 7–17. DOI:10.1016/J.ANBEHAV.2014.09.023

van Schaik, C. P. (2013). The costs and benefits of flexibility as an expression of behavioural plasticity: a primate perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1618). DOI:10.1098/rstb.2012.0339

van Schaik, C. P., Isler, K., & Burkart, J. M. (2012). Explaining brain size variation: from social to cultural brain. *Trends in Cognitive Sciences*, 16(5), 277–284. DOI:10.1016/j.tics.2012.04.004

van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Reviews Ecological Systems*, 24, 353–377. DOI:10.1146/annurev.es.24.110193.002033

van Woerden, J. T., van Schaik, C. P., & Isler, K. (2010). Effects of seasonality on brain size evolution: evidence from strepsirrhine primates. *The American Naturalist*, 176(6), 758–767. DOI:10.1086/657045

Vashro, L., & Cashdan, E. (2014). Evolution and human behavior spatial cognition, mobility, and reproductive success in northwestern Namibia. *Evolution and Human Behavior*, 36(2), 123–129.

Visalberghi, E., Sirianni, G., Fragaszy, D., & Boesch, C. (2015). Percussive tool use by Taï western chimpanzees and fazenda boa vista bearded capuchin monkeys: a comparison. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1682), 20140351. DOI:10.1098/rstb.2014.0351

von Frisch, K. (1967). *The Dance Language and Orientation of Honeybees.* Cambridge: Harvard University Press.

Wall, J., Douglas-Hamilton, I., & Vollrath, F. (2006). Elephants avoid costly mountaineering. *Current Biology*, 16(14), R528–R529. DOI:10.1016/j.cub.2006.06.049

Wang, R. F., & Spelke, E. S. (2000). Updating egocentric representations in human navigation. *Cognition*, 77(3), 215–250. DOI:10.1016/S0010-0277(00)00105-0

Ward, A., & Webster, M. (2016). Social foraging and predator-prey interactions. In A. Ward & M. Webster (Eds.), *Sociality: the behaviour of group-living animals* (pp. 55–89). DOI:10.1007/978-3-319-28585-6

Warren, S. D., Hohmann, M. G., Auerswald, K., & Mitasova, H. (2004). An evaluation of methods to determine slope using digital elevation data. *Catena*, 58(3), 215–233. DOI:10.1016/j.catena.2004.05.001

Warren, W. H. (2019). Non-Euclidean navigation. *The Journal of Experimental Biology*, 222, jeb187971. DOI:10.1242/jeb.187971

Watts, D. P. (1998). Seasonality in the ecology and life histories of mountain gorillas (*Gorilla gorilla beringei*). *International Journal of Primatology*, 19(6), 929–948. DOI:10.1023/A:1020366018187

Webb, P. W. (1984). Body form, locomotion and foraging in aquatic vertebrates. *Integrative and Comparative Biology*, 24(1), 107–120. DOI:10.1093/icb/24.1.107

Wehner, R., & Menzel, R. (1990). Do insects have cognitive maps? *Annual Reviews in Neurosciences*, 13, 403–417.

Wehner, R., & Wehner, S. (1990). Insect navigation: use of maps or Ariadne's thread? *Ethology Ecology & Evolution*, 2(1), 27–48. DOI:10.1080/08927014.1990.9525492

Westley, P. A. H., Berdahl, A. M., Torney, C. J., & Biro, D. (2018). Collective movement in ecology: from emerging technologies to conservation and management. *Proceedings of the Royal Society B: Biological Sciences*, 373, 20170004. DOI:10.1098/rstb.2017.0004

Wiebes, J. T. (1979). Co-evolution of figs and their insect pollinators. *Annual Reviews Ecological Systems*, 10, 1–12.

Wiener, J., Shettleworth, S., Bingman, V. P., Cheng, K., Healy, S., Jacobs, L. F., … Newcombe, N. S. (2011). Animal navigation: a synthesis. In R. Menzel & J. Fischer (Eds.), *Animal thinking* (pp. 51–76). Cambridge, MA: The MIT Press.

Wildgen, W. (2004). *The evolution of human language: scenarios, principles, and cultural dynamics* (W. Wolfgang, Ed.). Amsterdam: John Benjamins.

Willems, E. P., Barton, R. A., & Hill, R. A. (2009). Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. *Behavioral Ecology*, 20(5), 985–992. DOI:10.1093/beheco/arp087

Wilson, A. M., Hubel, T. Y., Wilshin, S. D., Lowe, J. C., Lorenc, M., Dewhirst, O. P., … West, T. G. (2018). Biomechanics of predator-prey arms race in lion, zebra, cheetah and impala. *Nature*, 554(7691), 183–188. DOI:10.1038/nature25479

Wilson, R. F., Marsh, H., & Winter, J. (2007). Importance of canopy connectivity for home range and movements of the rainforest arboreal rigntail possum (*Hemibelideus lemuroides*). *Wildlife Research*, 34(3), 177–184. DOI:10.1071/WR06114

Wiltschko, R., & Wiltschko, W. (2013). The magnetite-based receptors in the beak of birds and their role in avian navigation. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 199(2), 89–98. DOI:10.1007/s00359-012-0769-3

Wittig, R. M., & Crockford, C. (2018). Chimpanzees: investigating cognition in the wild. In N. Bueno-Guerra & F. Amici (Eds.), *Field and laboratory methods in animal cognition* (pp. 119–145). DOI:10.1017/9781108333191.008

Wittman, J., & Aukema, B. (2019). Foliage type and deprivation alters the movement behavior of late instar European Gypsy moth *Lymantria dispar* (Lepidoptera: Erebidae). *Journal of Insect Behaviour*, 32(1), 24–37. DOI:10.1007/s10905-019-09711-2

Yorzinski, J. L. (2017). The cognitive basis of individual recognition. *Current Opinion in Behavioral Sciences*, 16, 53–57. DOI:10.1016/j.cobeha.2017.03.009

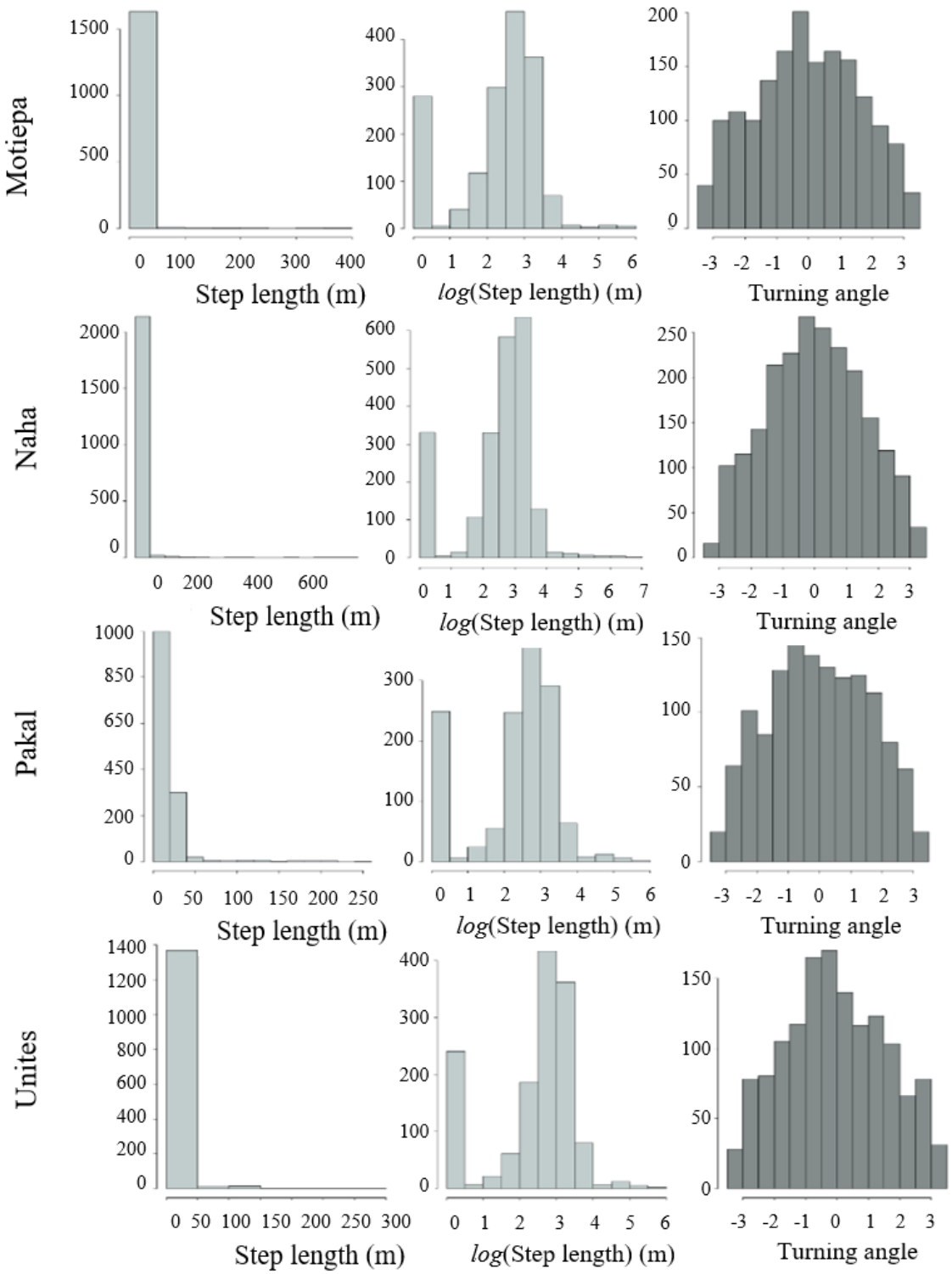
Youlatos, D., Couette, S., Halenar, L. B., Youlatos, D., Couette, S., & Halenar, L. B. (2015). Morphology of howler monkeys: a review and quantitative analyses. In M.M. Kowalewski, P. A. Garber, L. Cortes-Ortiz, B. Urbani, & D. Youlatos (Eds.), *Howler monkeys: behavior, ecology, and conservation* (pp. 133–176). DOI:10.1007/978-1-4939-1957-4_6

Zuberbhüler, K., & Janmaat, K. M. R. (2010). Foraging cognition in nonhuman primates. In M. L. Platt & A. A. Ghazanfar (Eds.), *Primate neuroethology* (pp. 64–83). New York, US: Oxford University Press.

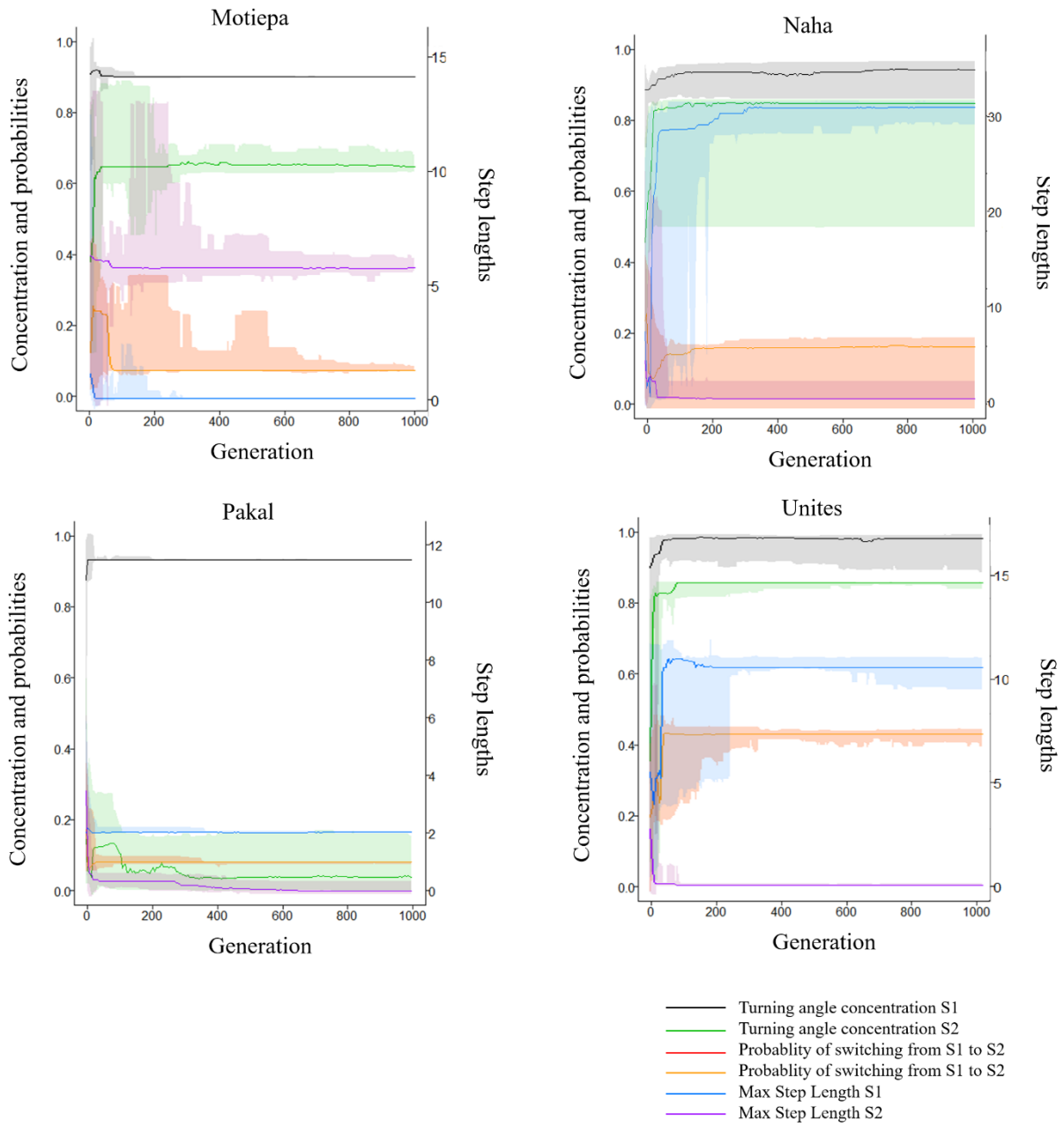
Zuberbühler, K., & Byrne, R. W. (2006). Social cognition. *Current Biology*, 16(18), R786–R790.

Appendix I

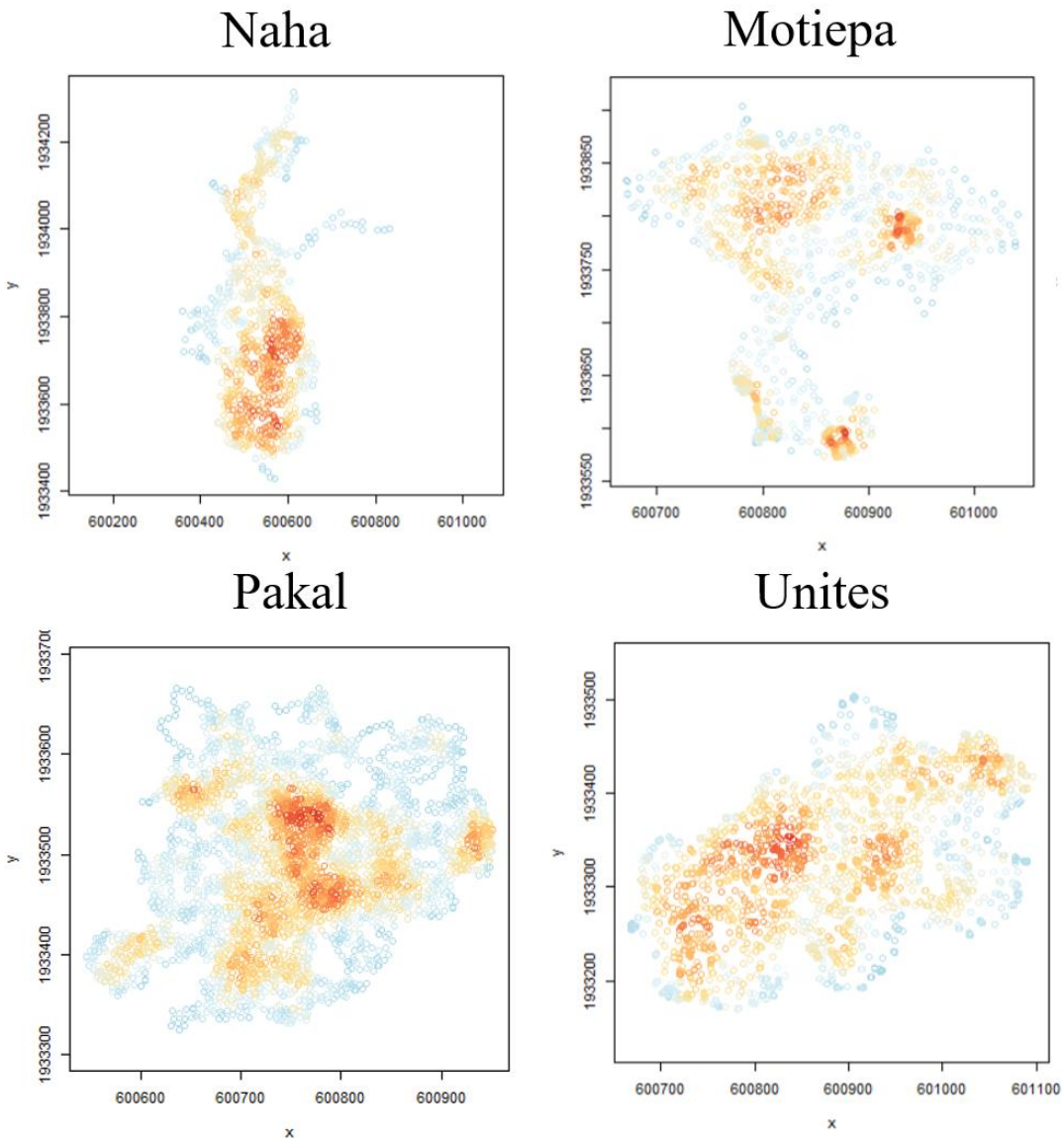
Appendix I. Figure 1 Step length and turning angles of the recorded trajectories for the study groups of black howler monkeys at PNP that were used to simulate random-walk movements.



Appendix I. Figure 2 Evolution of the optimised set of input parameters along the "adjustModel" ("SiMRiv" 1.0.3 R-package) algorithm's generation. These plots determine that the final solutions converged into stable values indicating that the algorithm succeed in replicating the real trajectory.



Appendix I. Figure 3 Number of times that each simulated correlated-random walk agent visited the same location within the constrains of the home range of the study group. Calculations were done using the R-package *recurse* and with the function "getRecursions" (Bracis et al., 2018)



Appendix II

Appendix II. Table 1. Total feeding time and overall percentage of time spent by black howler monkeys on the top ten tree species at Palenque National Park.

Species	Time (*min*)	Percentage
Poulsenia armata	8824	14.8
Ficus yoponensis	8342	14.0
Brosimum alicastrum	4962	8.4
Ficus aurea	2946	4.9
Ficus americana	2929	4.9
Acacia glomerosa	2891	4.8
Ficus insipida	2738	4.6
Ficus maxima	2323	3.9
Ficus crassinervia	1559	2.6
Ficus pertusa	1521	2.6

Appendix II. Table 2. Clustering analyses to determine the spatial patterns of black howler monkeys' preferred tree species. The nearest neighbour analysis examines the distance between each FT and the closest FT to it. and then compares such distance to expected values of a random sample of points. The nearest neighbour index (NNI) is the sum of all distances divided by the total number of points (1 = random distribution; >1 = cluster distribution; and. <1 = dispersed distribution). A negative Z-score indicates clustering while a positive Z-score indicates dispersion or evenness.

Tree_sp	Group	Observed distance (m)	Expected distance (m)	NN index	Z-Score
Acacia	Motiepa	16.6	23.9	0.70	-2.95
	Naha	67.5	56.1	1.12	1.23
	Pakal	143.2	68.8	2.08	4.63*
	Unites	28.2	27.9	1.01	0.06
Brosimum alicastrum	Motiepa	30.9	28.1	1.16	1.38
	Naha	16.2	20.7	0.78	-2.76
	Pakal	16.0	19.3	0.83	-2.72
	Unites	16.1	17.6	0.96	-0.61
Ficus spp.	Motiepa	16.2	23.1	0.70	-2.91
	Naha	22.6	29.4	0.76	-3.13
	Pakal	21.0	24.6	0.85	-1.93
	Unites	27.9	27.1	1.03	0.32
Poulsemia armata	Motiepa	10.1	14.9	0.72	-5.91*
	Naha	14.6	23.3	0.62	-6.75*
	Pakal	13.4	15.3	0.88	-2.17
	Unites	29.0	25.9	1.12	1.07

significant*

Appendix II. Table 3. The comparison between the number of real FTs and simulated locations that fell within a series of buffers between 5 and 20 metres traced from the route networks of the study groups was always significant. The number of FTs that fell within the buffers was always between 2.15 and 9.6 standard deviations higher than the number of simulated locations.

Group	Buffer (m)	N Real FTs	N simulated locations	*z*-score	*p*-value
Motiepa	5	113	66	6.90	<0.001
	10	154	120	4.67	<0.001
	15	184	159	3.82	<0.001
	20	196	184	2.15	0.016
Naha	5	123	75	6.95	<0.001
	10	177	129	6.71	<0.001
	15	192	161	5.04	<0.001
	20	203	178	4.66	<0.001
Pakal	5	132	66	9.60	<0.001
	10	186	121	8.66	<0.001
	15	207	188	3.40	<0.001
	20	220	160	8.67	<0.001
Unites	5	73	45	5.29	<0.001
	10	99	79	3.44	<0.001
	15	114	103	2.35	0.009
	20	125	118	1.88	0.029

Appendix II. Table 4. Results of the LMM testing differences among the number of locations computationally simulated and marked FT that fell within the visual detection distance of black howler monkeys.

Predictor variable	**Est.**	**s.e.**	***p*-value**
(Intercept)	150.2	16.4	[a]
Type of location (FT or simulated location)	-34.2	6.9	**< 0.001**
Buffer size	30.3	5.6	**< 0.001**

Random effect	**Term[1]**	**Standard deviation**
Group ID	(Intercept)	31.58
Group ID	Type of location (FT or simulated lcoation)	11.44

Number of observations = 32; number of levels of random effects: Group IDs = 4

[1] The column 'term' specifies whether the row refers to a random intercept or random slope component.

Appendix II. Table 5. Results of the LMM testing for differences in the number of FTs visually intercepted per metre travelled along route segments with different usage frequency (e.g., twice, 3 times, … until 9 times).

Predictor variable	**Est.**	**s.e.**	***p*-value**
(Intercept)	-2.43	0.22	[a]
Times used	0.35	0.04	**< 0.001**
Buffer size	0.36	0.92	**< 0.001**

Random effect	**Term[1]**	**Standard deviation**
Group ID	(Intercept)	0.42
Group ID	Times used	0.03
Group ID	Buffer 5 m	0.04
Group ID	Buffer 15 m	0.02
Group ID	Buffer 20 m	0.00

Number of observations = 116; number of levels of random effects: Group IDs = 4

[1] The column 'term' specifies whether the row refers to a random intercept or random slope component.

Appendix II. Table 6. Results of the full GLMM testing the influence of different landscape attributes (slope. presence of canopy gaps, elevation and visibility of feeding trees[1]) on the occurrence of a route segment used at least twice within a certain quadrat.

Predictor variable	**Est.**	**s.e.**	***p*-value**
(Intercept)	-31.26	0.29	[a]
Slope	0.39	0.14	0.005
Presence of canopy gaps	0.35	0.19	0.057
Elevation	-0.26	0.12	0.032
Visibility of FT[1]	-0.59	0.11	< 0.001
Elevation * Visibility of FT[1]	-0.44	0.14	0.002
Overlapping area [b]	-0.74	0.20	< 0.001
Location within the HR [b]	-0.72	0.50	0.147
Autocorrelation term [b]	29.43	0.10	< 0.001

[a] Not shown because of having no meaningful or very limited interpretation.

[b] Represent control predictors included in the model

Appendix II. Table 7. Random slopes and estimated variance components (standard deviations) for the random effects and residuals from the model testing the influence of landscape attributes on the occurrence of routes used at least twice within a quadrant.

Random Effect	Term[1]	Standard deviation
Group ID	(Intercept)	1.25
Group ID	Slope	0.00
Group ID	Presence of canopy gaps	0.16
Group ID	Elevation	0.67
Group ID	Visibility of FT	0.41
Group ID	Elevation * Visibility of FT	0.35
Group ID	Overlapping area	0.00
Group ID	Location within the HR	0.95
Group ID	Autocorrelation term	0.00

Number of observations = 5037; number of levels of random effects: Group IDs = 5

[1] The column 'term' specifies whether the row refers to a random intercept or random slope component.

Appendix II. Table 8. Results of the full GLMM testing the influence of different landscape attributes (slope, presence of canopy gaps, elevation and visibility of feeding trees[1]) on the occurrence of a route segment used at least four times within a certain quadrat.

Predictor variable	**Est.**	**s.e.**	***p*-value**
(Intercept)	-31.26	0.29	[a]
Slope	0.39	0.14	0.005
Presence of canopy gaps	0.35	0.19	0.057
Elevation	-0.26	0.12	0.032
Visibility of FT[1]	-0.59	0.11	< 0.001
Elevation * Visibility of FT[1]	-0.44	0.14	0.002
Overlapping area [b]	-0.74	0.20	< 0.001
Location within the HR [b]	-0.72	0.50	0.147
Autocorrelation term [b]	29.43	0.10	< 0.001

[a] Not shown because of having no meaningful or very limited interpretation.

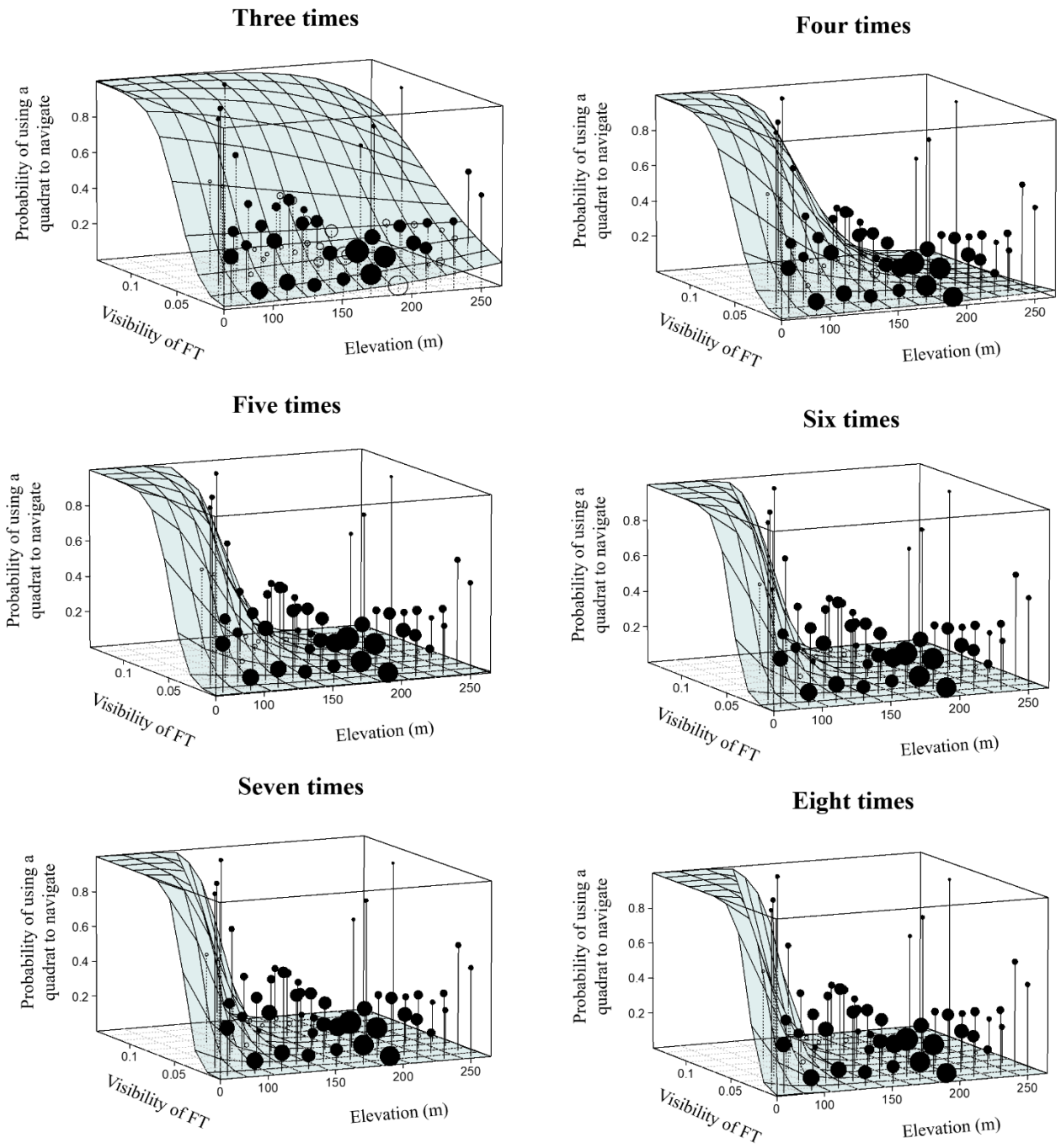
[b] Represent control predictors included in the model

Appendix II. Table 9. Random slopes and estimated variance components (standard deviations) for the random effects and residuals from the model testing the influence of landscape attributes on the occurrence of routes used at least four times within a quadrant.

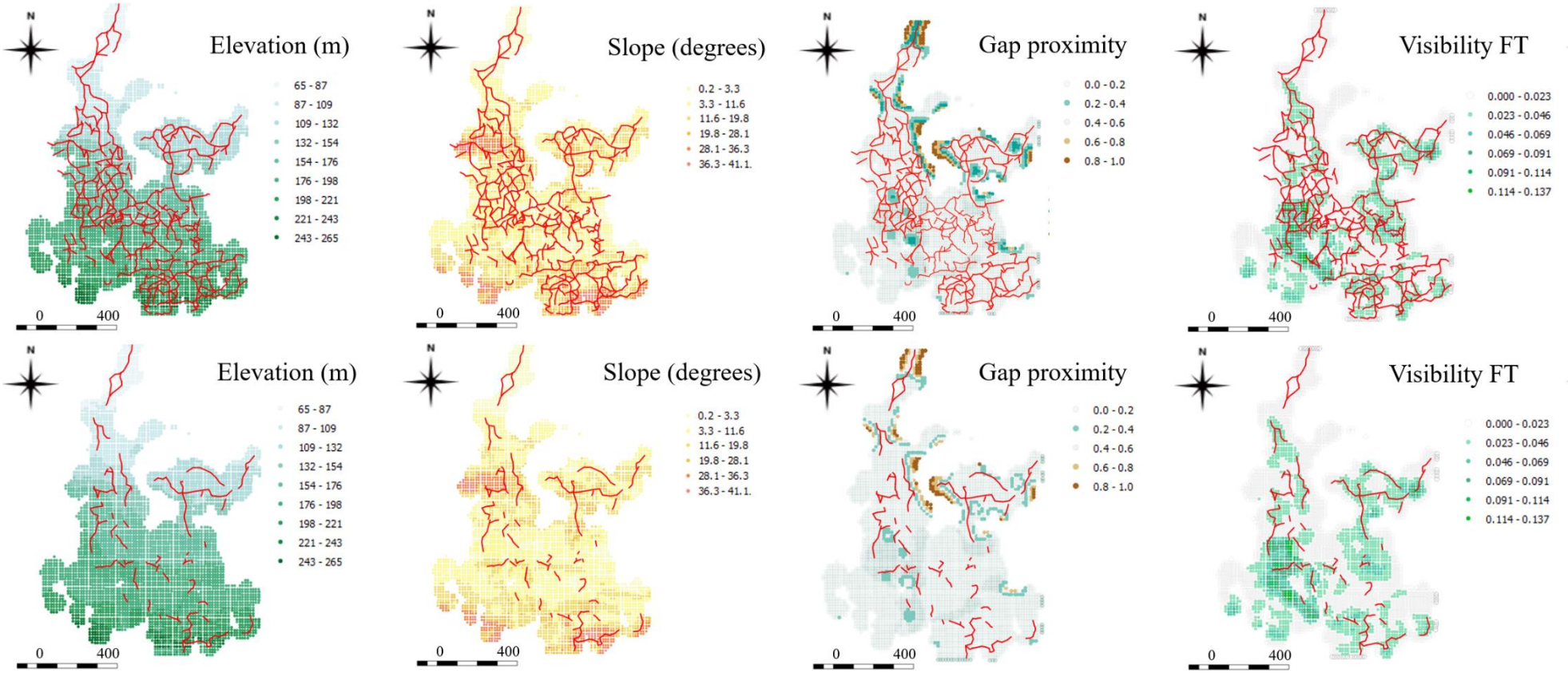
Random Effect	Term[1]	Standard deviation
Group ID	(Intercept)	0.70
Group ID	Slope	0.00
Group ID	Presence of canopy gaps	0.24
Group ID	Elevation	0.00
Group ID	Visibility of FT	0.00
Group ID	Elevation * Visibility of FT	0.22
Group ID	Overlapping area	0.00
Group ID	Location within the HR	1.05
Group ID	Autocorrelation term	0.00

Number of observations = 5037; number of levels of random effects: Group IDs = 5

[1] The column 'term' specifies whether the row refers to a random intercept or random slope component.



Appendix II. Figure 1 Probability that black howler monkeys selected a quadrat to navigate in between three and height different occasions in relation to the relative elevation within their home range and the visibility of FT. The interaction was not significant for routes used at least three times but was always significant for routes used more than three times. The height of spheres represents the probability that a certain quadrat was chosen to navigate per combination of elevation and visibility of FT. Each surface (i.e., square) represents the expected probability of a quadrat to be chosen according to the model (conditional on all other predictors being set at their average value). Sphere size corresponds to the relative number of observations, with closed circles being above the model surface and open circles below.



Appendix II. Figure 2 Estimated range of influence of landscape attributes on the location of habitual routes in which each data point corresponds to a quadrant within the study home ranges.

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Movement Ecology

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Arboreal route navigation in a Neotropical mammal: energetic implications associated with tree monitoring and landscape attributes

Miguel de Guinea[1*], Alejandro Estrada[2], K. Anne-Isola Nekaris[1] and Sarie Van Belle[3]

Abstract

Background: Although navigating along a network of routes might constrain animal movement flexibility, it may be an energetically efficient strategy. Routinely using the same route allows for visually monitoring of food resources, which might reduce the cognitive load and as such facilitate the process of movement decision-making. Similarly, locating routes in areas that avoid costly landscape attributes will enhance their overall energy balance. In this study we determined the benefits of route navigation in an energy minimiser arboreal primate, the black howler monkey (*Alouatta pigra*).

Methods: We monitored five neighbouring groups of black howler monkeys at Palenque National Park, Mexico from September 2016 through August 2017. We recorded the location of the focal group every 20 m and mapped all travel paths to establish a route network ($N = 1528$ travel bouts). We constructed linear mixed models to assess the influence of food resource distribution ($N = 931$ trees) and landscape attributes (slope, elevation and presence of canopy gaps) on the location of routes within a route network.

Results: The number of food trees that fell within the visual detection distance from the route network was higher (mean: 156.1 ± SD 44.9) than randomly simulated locations (mean: 121.9 ± SD 46.4). Similarly, the number of food trees found within the monkey's visual range per meter travelled increased, on overage, 0.35 ± SE 0.04 trees/m with increasing use of the route. In addition, route segments used at least twice were more likely to occur with increasing density of food resources and decreasing presence of canopy gaps. Route segments used at least four times were more likely to occur in elevated areas within the home ranges but only under conditions of reduced visual access to food resources.

Conclusions: Route navigation emerged as an efficient movement strategy in a group-living arboreal primate. Highly used route segments potentially increased visual access to food resources while avoiding energetically costly landscape features securing foraging success in a tropical rainforest.

Keywords: Landscape, Navigation, Route selection, Cognitive load, Black howler monkey (*Alouatta pigra*), Topological cognitive map, Route-based spatial map

* Correspondence: mdeguinea@gmail.com
[1]Department of Social Sciences, Oxford Brookes University, Gibbs Building, Gipsy Lane, Oxford OX3 0BP, UK
Full list of author information is available at the end of the article

Background

Animal movement strategies are influenced by individuals' ability to acquire and process information, as well as the energetic requirements of traveling through the landscape [1–3]. Some animal species have been suggested to navigate using cognitive maps: mental representations coding spatio-temporal information of the space where they live in that permits efficient movement decisions [4–8]. Although the elements that construct such spatial representation are still debated [8], the ability to navigate flexibly in space has been suggested to be indicative of sophisticated cognitive maps and, hence, enhanced cognitive abilities [9]. For instance, some animal species have been suggested to compute distances and angles based on features of the landscape as in an Euclidean representation of the area (e.g., honey-bees, *Apis melifera*, [10], African elephants, *Laxodonta africana*, [11], chimpanzees, *Pan troglodytes*, [9]). Contrarily, the most common navigation strategy associated with cognitive maps is the repeated use of paths, here referred to as "habitual routes" (insects [12], birds, [13], mammals, [14, 15], humans, [16]). By following an established set of habitual routes animals and humans benefit from simplifying the decision-making process of movement while still securing foraging success [17].

Even though navigating along habitual routes constrains an animal's movement flexibility, it may nonetheless enhance its overall energy balance by selecting specific areas along which to navigate that minimize the energetic costs of movement [18]. The accumulation through generations of environmental information within a group of animals can minimise the cost of travelling by optimising the selection of routes to navigate [19]. For instance, pigeons (*Columba livia*) that travelled in pairs increased the linearity of their homing route over the course of multiple generations [19]. Similarly, translocated bighorn sheep (*Ovis canadiensis*) adjusted the location of their migratory routes over time in order to avoid energetically costly areas of the landscape [20]. Combining experiences of several individuals permits foragers not only to efficiently locate resources but also to select the closest or most profitable ones [21]. For example, in ants (*Linepithema humile*), sharing information among group member via pheromone concentration along paths favoured the selection of shorter paths towards food resources [22]. Hence, even though habitual route navigation is frequently hypothesized to be a limiting navigation strategy associated with inferior cognitive skills [6], accumulating and sharing information within groups can lead to the selection of routes that enhance foraging [23] while economising the cost of traveling (avoiding costly landscape features such as mountain ridges [24], and predators, [25]). Additionally, animals with sophisticated cognitive skills might still travel along recurrently used routes because these provide an energetically efficient strategy to navigate [26].

A major potential advantage associated with using habitual route segments is the ability to monitor regularly the phenological states of food resources that are located within animals' visual range while travelling [18, 27]. Habitual route navigation requires the animal to memorize a series of familiar landmarks (i.e., environmental features) to orientate their movements and relocate feeding and resting sites [28, 29]. The complexity of the cognitive process underlying movement decision-making will increase with the total number of locations to be remembered (e.g., landmarks, food sources; hereafter cognitive load, [30]). Hence, animal's cognitive load should decrease considerably when only needing to associate multiple food resources with a limited set of travel routes [31, 32]. Reduction in cognitive load may decrease the amount of energy allocated to brain tissue, which in turn can be employed for other physiological processes and/or behavioural activities [33]. Additionally, by clustering the food resources along routes, animals would decrease the energy spent on travelling when searching for food [18].

Similarly, the structure of the area or landscape that is traversed by an animal or a group is undoubtedly linked to the energetic cost of locomotion [34]. Different features of the landscape, such as slope, elevation or substrate, determine the energetic cost of locomotion through an area, which in turn will influence the location of frequently used routes [3, 34]. In terrains with steep slopes, terrestrial animals need to increase their kinetic energy as they move up a slope, increasing the biomechanical and metabolic cost of moving [34, 35]. For instance, Newmark & Rickart [14] showed that wild ungulates (*Odocoileus hemionus* and *Cervus elaphus*) repeatedly used routes that avoided steep slopes to economise energetic expenditure. Likewise, slope at the ground level may influence the movement of animals at the tree level [36]. Arboreal animals were shown to include ground slope into their movement decisions potentially to reduce the cost of travelling, similar to terrestrial animals, assuming a net gain in elevation at the ground is mirrored at the level of tree crowns [37, 38]. In contrast, detectability of further away food resources and neighbouring conspecific groups while travelling may increase in more elevated areas within animal's home range [18]. Incorporating visual information into movement decisions during travelling likely enhances both terrestrial and arboreal animals' foraging efficiency and home range defensibility [1, 39].

Lastly, the characteristics of the substrate are important determinants of the energy expenditure for an animals as well [3, 40]. In case of arboreal animals, the characteristics of the substrate, specifically the degree of

lateral connectivity, not only influence movement costs but also the availability of substrate itself (i.e., presence of canopy gaps in the forest or deforested areas [41]). McLean et al., [41] demonstrated that crown thickness and density were unifying parameters driving the selection of movement in arboreal animals with different locomotor strategies, which highlights the transversal importance of lateral connectivity in arboreal navigation. Similarly, descending to the ground and re-ascending into trees was shown to increase exponentially the biomechanical costs of movement both in orangutans (*Pongo pygmaeus*, [36]) and human parkour athletes [42]. Optimising the energetic performance during arboreal locomotion likely requires selecting highly interconnected tree sequences and avoid canopy gaps to navigate [41].

Here, we explore different factors that influence the location of habitual routes of an "energy minimiser" [43], group-living arboreal primate, the black howler monkey (*Alouatta pigra*, hereafter black howlers). The slow transit and long retention times in the digestive system associated with black howlers' leaf-based diet reduces the availability of metabolic energy [17]. In addition, black howlers engage in highly selective foraging patterns to fulfil their nutritional demands using many different individual trees to forage that vary both within and between years [44]. Memorising all these locations and their respective phenological cycles is assumed to be challenging given the relatively small brain size of these primates [17]. By locating travel routes near potential food resource, black howlers may benefit from reducing their cognitive load by continuously monitoring the status of food resources while travelling [45]. Further, the study was conducted in a terrain where topographic features vary sharply. The influence of elevation changes and occasional gaps of forest coverage could be influencing the movement decisions of black howlers [41, 45]. Hence, the location of habitual routes to navigate is expected to reflect the energy minimising strategy of black howlers by avoiding such costly attributes of the landscape.

First, we hypothesised that black howlers locate their routes along tree sequences that would allow them to visually inspect food resources. We predicted that the number of food resources that fell within the estimated visual range of black howlers would be higher within habitual route segments than at locations outside the route network. Moreover, the number of food resources that can be visually intercepted per metre travelled would increase with a route's usage frequency. Second, we hypothesised that the location of routes would allow black howlers to avoid costly features of the landscape. We predicted that terrain slope and canopy gaps would negatively influence the occurrence of routes while elevation would have a positive effect only in areas where food trees are less abundant. Overall, we aim to gain insights into the route selection process in arboreal navigation by exploring the benefits associated with travelling frequently along the same tree sequences.

Materials and methods

Study site and subjects

We conducted the study in Palenque National Park (PNP, 17°29′N-92°02′W), Mexico, which covers 1171 ha. PNP has a variable terrain due to geological formations and the remains of Mayan ruins underneath the forest floor [46, 47]. As a result, the study area ranges between 65 and 264 m above sea level and the maximum slope of the terrain across the study groups was 41.2 degrees (Table 1). The area covered by canopy gaps (i.e., pasturelands, fallen trees, roads) within the study area was 3.7 ha (7% of the total study area).

From September 2016 through August 2017, we observed five groups of wild black howlers, four consecutive days per week (two groups each day) for a total of 297 days and 3104 contact hours (Balam: 58 d, 571 h; Motiepa: 58 d, 628 h; Naha: 63 d, 631 h; Pakal: 61 d, 650 h; Unites: 59 d, 622 h). We designed the data collection protocol such that we sampled the same group only every two or three weeks, leaving a window of one or two weeks in between sampling weeks to control for the productivity of certain tree species.

Data collection

During observation days (ca. 05:30–17:00), we conducted instantaneous scan samples at 15 min intervals to record the behaviour of all visible group members, as well as the coordinates of the location of the estimated centre of the group using a GPS Garmin 64S (mean GPS error: 6.6 ± SD 2.3 m). In order to obtain detailed information on feeding behaviour, we recorded a feeding bout whenever one or more individuals fed on a plant for a minimum of 5 min accumulated across of feeding individuals (e.g., one individual for 5 min, two individuals each for 3 min, five individuals each for 1 min). For each feeding bout, we recorded the item fed on, the plant species, and at 3 min intervals the number of individuals feeding. We used these feeding bout data to identify the top 10 food species of black howlers at PNP based on the percentage of time spent feeding on each species (*Poulsemia armata*, *Ficus spp.* (6 species), *Brosimum alicastrum*, and *Acacia glomerosa*; see Additional file 1: Table S1). Subsequently, we searched and marked all individual trees (hereafter FTs) with a DBH (diameter at breast height) ≥ 10 cm, including those that groups did not feed on, from these species throughout the home ranges of the study groups (Balam: $N = 137$; Motiepa: $N = 220$; Naha: $N = 213$; Pakal: $N = 227$; Unites: $N = 134$).

Table 1 Demographic and environmental summary of the study groups and areas: number of individuals present in each group during the study period; estimated home range size using Kernel 95% estimator; mean number of feeding trees (N FTs) visually detected from the route network till 20 m distance; elevation and slope range within each study group; and, area covered by canopy gaps in hectares and percentages for each study group

Group ID	Group size	HR size (ha)	N FTs visually detected (mean ± SD)	Elevation range (m) (min - max)	Slope range (°) (min - max)	Gaps (ha) (% coverage)
Balam	3–4	10.3	–	170.5–260.0	0.6–39.4	0.3 (3%)
Motiepa	6–8	7.1	161.8 ± 36.9	96.4–173.8	0.3–29.4	0.9 (12.9%)
Naha	5–8	15.3	173.8 ± 35.5	65.0–190.4	0.2–45.2	1.8 (11.9%)
Pakal	7–9	10.6	186.3 ± 38.8	152.6–212.8	0.6–29.4	0.3 (3%)
Unites	4	8.6	102.8 ± 22.5	178.1–264.9	1.5–40.9	0.3 (3.3%)

We recorded a travel bout whenever two or more group members moved into a neighbouring tree or further until at least two members of the group engaged in a stationary activity different from that in the original tree (i.e., howling, resting or foraging, [48]). In this species, collective group movement is very conspicuous and is typically initiated by an individual leaving the tree and immediately followed by all other group members in a single line progression [48]. Throughout travel bouts, we recorded GPS locations of the estimated group centre every 20 m.

Data analyses

We estimated the home range of the study groups using the R package *adehabitatHR* 0.4.15 and the kernel density estimation (KDE) method based on the geographic coordinates recorded during scan samples [49]; Fig. 1). We defined a group's home range as the 95% KDE isopleth and a core area as the 50% KDE isopleth [48].

In order to construct a habitual route network, we first overlaid all daily travel paths recorded during the same week per group onto a raster map of the area and checked their concordance [18]. Whenever a daily path fell within a 10 m buffer of another daily path of that week for at least 15 m without deviating more than 45° from the other path, we considered it as the same travel segment [11]. We selected these parameters in order to be consistent with previous research [18, 51–53] and to control for GPS accuracy and travel directionality [52, 53]. Food resources in rainforests can occur for a short period in the same location within the same week [54], which can lead to an overestimation of the frequency of used routes [51]. Hence, we first constructed "weekly paths" including only unique daily paths of each sampled week to avoid a bias towards re-used route segments due to short revisiting intervals to certain FTs within that same week. Each group's weekly paths were overlaid on top of each other and we repeated the same procedure as described above to determine across how many weeks route segments were used [11]. We defined the habitual route network of each group as path segments used during at least two separate observation weeks.

We determined the influence of FT's distribution on the location of the route networks by simulating the same number of recorded FTs per study group randomly distributed within their respective home ranges, excluding areas with no forest cover [55]. We did not include any cluster parameter into our simulations since most of the tree species were distributed randomly within the study area (*Z*-scores: *Poulsemia armata*, − 3.4; *Ficus spp.*, − 1.9; *Brosimum alicastrum*, − 0.7; and, *Acacia glomerosa*, 0.7; for details see Additional file 1: Table S2, [56]). We ran 10,000 simulations using the R package *rgdal* 1.3–6 [57] and the function "spsample". Finally, a series of buffers with 5 m increment from 5 m to 20 m were traced around habitual routes of each study group, and the total number of recorded FTs and simulated FTs that fell within each buffer was calculated and statistically compared (see below, [44]). Since we performed 10,000 simulations, we calculated the mean number of simulated FTs that fell within each buffer for each study group to compare it with the number of observed FTs (in Additional file 1: Table S1, we provide the fraction of FTs that fell above the number of simulated location for each buffer). Subsequently, we tested whether the number of FTs that fell within the buffers created along habitual route segments increased with the frequency these routes were reused. For this, we calculated the number of FTs intercepted per meter travelled along each segment to account for segment length.

We determined the topographic attributes of the landscape using an archaeological map of the Mayan city of Palenque [46]. We georeferenced this topographic map, which had a resolution of 4 m, and triangulated the three-dimensional locations into ArcMap 10.4 to create a TIN layer that was converted into a Digital Elevation Model (DEM). We georeferenced the TIN version of the map using 15 salient features of the landscape (e.g., roads, Mayan ruins) visible both on the archaeological map and freely available satellite layers. We overlaid a grid layer of 10×10 m^2 quadrats and extracted values for slope and elevation for each quadrat using the Spatial Analysist tool from ArcMap 10.4. For elevation, we

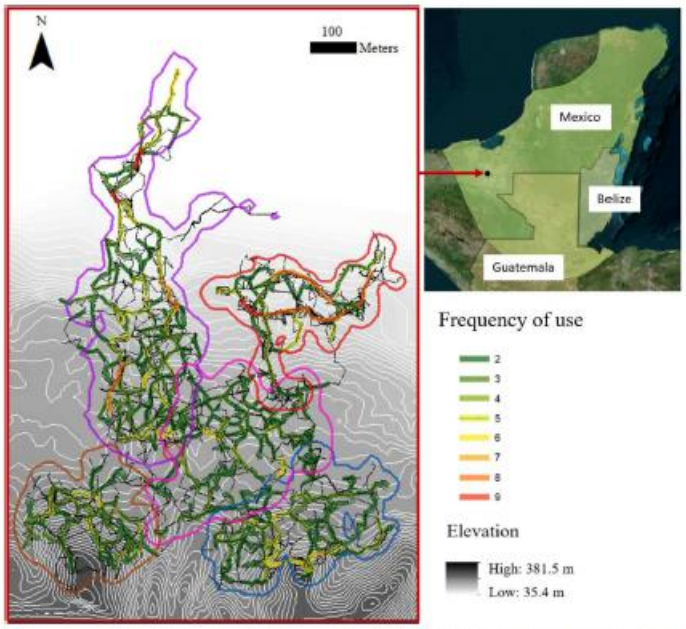

Fig. 1 Home ranges (95% kernel density estimates) of five study groups of black howler monkeys at Palenque National Park (Naha: *purple*; Motiepa: *red*; Pakal: *pink*; Balam: *brown*; Unites: *blue*) overlaid on top of elevation contour lines (white lines). Within the home ranges of each study group, we show all recorded travel bouts (black continuous lines), as well as the frequency (green-red scale) that travel segments were used. The geographic distribution of *Alouatta pigra* is shown in the top right of the figure (data from IUCN [50])

determined the height at the centre of each quadrat. For slope, we calculated the maximum rate of change in elevation for each quadrat relative to its adjacent quadrats [58]. We marked the edges of canopy gaps in the field using a GPS device and corrected them using satellite imagery. We used remotely sensed images on land cover from NASA's Landsat 8 satellite for this purpose [59]. Subsequently we created a buffer of 25 m from the centre of each quadrat and calculated the percentage overlap between such a buffer and the recorded canopy gaps.

We determined the potential of visual inspection of FTs while travelling through habitual route segments by creating a series of buffers every 5 m from the centre of each quadrat up till 35 m, which is the estimated visual detection distance of howlers [17, 45]. We counted all marked FTs contained within each buffer including the FTs already counted in small buffers (e.g., when counting FTs contained within the 10 m buffer, we counted those contained within the 5 m buffer again). Subsequently, we divided the number of FTs contained in each buffer by the total number of FTs within the home range of the study group. We calculated these for the preferred tree species within each home range separately. Finally, per quadrat, values for all buffers were summed and divided by the number of buffers ($N = 7$). By including previously counted trees in smaller buffers into large buffers, we emphasised the importance of FTs near the centre of the cell. Thus, we calculated an index of FT's density near the centre of each quadrat as a measure for visual access to potential food resources (hereafter called "FTs density"; see Additional file 2: Figure S1; and, Additional file 3: Figure S2).

Statistical analysis

We conducted all statistical models in R 3.5.2 (R Core Team, 2018) and implemented them using the functions *lmer* and *glmer* of the *lme4* package 1.1–21 [60]. We fitted two LMMs to determine the influence of FTs on the location of routes used by black howlers.

First, we tested whether routes intercepted more FTs than by chance by using the number of locations intercepted per buffer around the route network as response variable and type of location (real or mean of simulated FTs) as predictor variable [model 1: N FTs ~ type of

location + buffer size + (1 + type of location + buffer size| group ID)]. For the second model, the response variable was the number of FTs intercepted per meter travelled and the frequency of use of a certain route segment was the predictor variable [model 2: *log*(N FTs per metre) ~ frequency of use of the segment + buffer size + (1 + frequency of use of the segment + buffer size | group ID)]. For both models, buffer size was used as a control variable since we would expect that larger buffers may intercept a larger number of FTs. We excluded one study group (Balam) from these two models because its composition and home range location changed in January 2017 [61].

In addition, we fitted two GLMMs with a binomial error structure and a logit link function instead of one with continuous outcome to test the influence of landscape features on the location of route segments. For these models, the response variable was the presence/absence of routes for each quadrat, either used at least twice or at least four times, respectively. Previous research highlighted that the characteristics of routes used at least twice and at least four times differed from each other [51]. Thus, we decided to construct separate models. For both models, the predictor variables were elevation, slope, percentage of area covered by gaps, and FTs density per quadrat. We included an interaction between elevation and FTs density in both GLMMs since we predicted that black howlers located routes to navigate in more elevated areas only when the visual access to food resources decreased.

To account for potential differences among groups, we included group ID as a random variable (random intercept) in all models. In order to allow for fixed effect predictors to vary among the levels of the random effect variables, random slope terms were included in the models as well. In addition, we incorporated two control variables: intergroup overlap (whether a certain quadrat was used by multiple groups or not) and home range location (whether the quadrat fell inside or outside the group's core area).

We controlled for spatial autocorrelation by determining an autocorrelation term from the full model and subsequently including this term as a control variable in a newly fitted full model [62]. These terms were calculated as the average of the residuals from the original model (for all data points from the same group) weighted by the distance to the particular data point. The weight followed a normal distribution for which the standard deviation (D) was optimised such that the log-likelihood of the full model including the autocorrelation term was maximised (here: $D = 5–7$; based on [62]) [model 3: presence of route ~ *sqrt* (slope) + presence of gap + elevation * FTs density + overlap + area (home range or core) + autocorrelation term + (1 + *sqrt* (slope) + presence of gap + elevation + FTs density + overlap + area + autocorrelation term + elevation: FTs density | | group ID)].

We verified that the residuals of the models were normally and homogeneously distributed by visually inspecting qq-plots and plotting them against fitted values. We also tested for multicollinearity by inspecting variance inflation factors using the *vif* function from the *car* package [63]. Similarly, we assessed the stability of the GLMMs by comparing the estimates derived from a model based on all data with those obtained from models based on subset which excluded levels of the random effects one at a time. No model assumptions were violated. In all cases, we compared the full model to a corresponding null model (with only random and control variables) using likelihood-ratio tests (*anova* function set to "Chisq"). When an interaction term had no significant effect, we ran a reduced model including only the main effects. Finally, if the likelihood-ratio test for full and null model comparison was significant, we inspected the significance of each predictor variable using likelihood- ratio tests comparing full models with reduced models without the variables of interest, using the *drop1* function [64].

Results

We recorded a total of 1528 travel bouts (mean: 305.6 ± SD 43.9 travel bouts per group). On average, the length of an individual travel bout was 65.3 ± SD 57.5 m and the daily path length was 365.8 ± SD 199.2 m, ranging from 28.2 m to 1022.8 m. Between 64.5 and 75.1% of the travel bouts fell within the habitual route network (paths used at least twice), which had a mean length of 3.2 ± SD 1.2 km per group (Fig. 1). Home range size ranged between 7.1–15.3 ha while the relative difference in elevation within each study group was 86.2 ± SD 24.8 m (Table 1).

Spatial distribution of food trees

The total number of FTs within the assumed visible detection range from the habitual route network (mean 156.1 ± SD 44.1 trees per group) was significantly higher than would be expected by chance (mean 122.0 ± SD 46.4 locations) as shown by the likelihood ratio test ($\chi^2 = 7.9$, Estimate = – 34.2 ± 6.9, df = 1, $P = 0.005$). Similarly, the number of FTs potentially visible from the habitual route network per metre travelled increased with increasing frequency of use of the segment (likelihood ratio test: $\chi^2 = 15.1$, Estimate = 0.4 ± 0.04, df = 1, $P < 0.001$). For instance, the number of FTs that fell within the estimated visual range along route segments used twice was 0.07 ± 0.04 trees/m while it increased to 0.11 ± 0.05 trees/m in segments used four times and to 0.24 ± 0.20 in segments used seven times (Fig. 2).

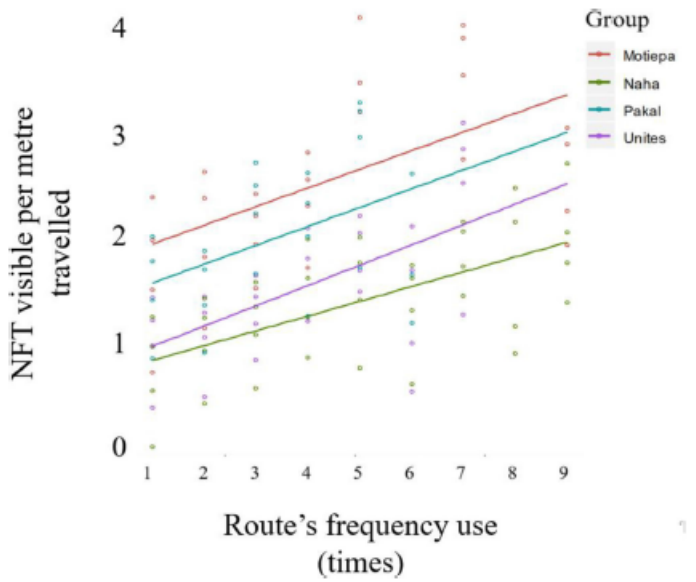

Fig. 2 Fitted linear regression of number of feeding trees (FTs) intercepted per metre travelled against frequency of use of route's segments. The plot shows the four study groups that were included in this analysis. Note that route segments used once were travel bouts that never overlapped other travel bouts

Landscape attributes

We found that the GLMMs for routes used at least twice and routes used at least four times provided a significantly better fit than the null models (Table 2). The probability of a quadrat containing a route that was used at least twice increased with FTs density but decreased with presence of canopy gaps. After removing a non-significant interaction from the full model (see Additional file 1: Table S1 for full model results), we did not find a significant influence of either elevation or slope on the probability of a quadrat containing a route used at least twice.

Similar to the previous model, routes used at least four times were significantly influenced by FTs density. Contrary to the previous model, there was not a significant influence of gap presence on the location of a route used at least four times. There was a significant effect of the interaction between elevation and FTs density in the model (Fig. 3). As we predicted, there was a positive effect of elevation only in areas with potentially low visual access to FTs. Even though the effect of slope in the model was not significant, there was a positive trend towards locating routes used at least four times in quadrats with highly pronounced slopes (Table 2).

Discussion

Our findings show that black howlers navigate along a habitual route network linked to the distribution of potential food resources and landscape attributes. While using specific routes to navigate limits an animal's movement options [65], black howlers seem to counteract such constraints by optimising the location of their habitual routes. Such knowledge, potentially accumulated over generations, may lead to the selection of routes that minimises energy expenditure and favours tree monitoring while traveling [1, 66].

Because of the logistical difficulties of observing monitoring behavior in arboreal animals (i.e., turning their head combined with fixed gaze towards food resources while travelling, [27]), we developed a method to infer the probability that arboreal animals monitored FTs while travelling through habitual routes. Such a measure considers the density of FTs nearby frequently used routes, and thus the potential visual access of those FTs. Our findings show that black howlers at PNP intercept a higher number of food resources within their visual range while travelling along their habitual route networks than they would be expected by chance. That is, the number of food resources visually intercepted

Table 2 Results of two GLMMs testing the influence of different landscape attributes (slope, presence of canopy gaps, elevation and FTs density) on the probability occurrence of a route segment used at least twice and four times within a certain quadrat. Group ID ($N = 5$) was included as random effect in the model. We compared the full model to a corresponding null model (with only random and control variables) using likelihood-ratio tests. All p-values < 0.05 are shown in bold for clarity

Response variable	Probability of locating a route used at least twice					Probability of locating a route used at least four times				
Full null model comparison	$\chi2 = 23.2$, d.f. = 5, $p < 0.001$					$\chi2 = 18.8$, d.f. = 5, $p = 0.002$				
Predictor variable	Est.	s.e.	CI_{lower}	CI_{upper}	p-value	Est.	s.e.	CI_{lower}	CI_{upper}	p-value
(Intercept)	−0.156	0.574	−1.567	1.209	a	− 3.126	0.298	−6.359	−2.531	a
Slope	0.139	0.104	−0.128	0.481	0.182	0.390	0.139	0.006	0.752	0.058
Presence of canopy gaps	−0.803	0.115	−1.088	−0.482	**0.001**	−0.354	0.186	−0.452	0.023	0.128
Elevation	0.446	0.328	−0.323	1.298	0.198	0.944	0.550	−0.363	2.237	0.173
FTs density	0.896	0.213	0.372	1.390	**0.006**	0.967	0.246	0.401	1.533	**0.010**
Elevation * FTs density	−0.280	0.210	−0.783	0.340	0.273	−0.439	0.140	−0.809	−0.374	**0.041**
Overlapping area [b]	0.274	0.136	−0.014	0.689	0.054	−1.000	0.203	−3.398	−0.437	**0.003**
Location within the HR [b]	−0.538	0.442	−1.609	0.518	0.255	−0.724	0.499	−1.414	0.838	0.190
Autocorrelation term [b]	2.487	0.072	2.347	2.632	**< 0.000**	2.943	0.100	1.636	3.252	**< 0.000**

[a]Not shown because of having no meaningful or very limited interpretation
[b]Represent control predictors included in the model

increased 19% with the number of times a certain route segment was used. These results are consistent with the hypothesis that black howlers use habitual route networks to facilitate the visual inspection of potential food resources [17, 45].

While travelling through areas with high FTs densities facilitates the potential monitoring of FTs, black howlers could also be enhancing their foraging success by gaining access to FTs. However, the high reusage frequency of some route segments makes it unlikely that food was always available every time they travelled along that specific route. Furthermore, we did not only include in the analyses trees in which we observed monkeys feed but all trees from preferred tree species present in the study area from which they did not feed during our observations. Therefore, black howlers potentially

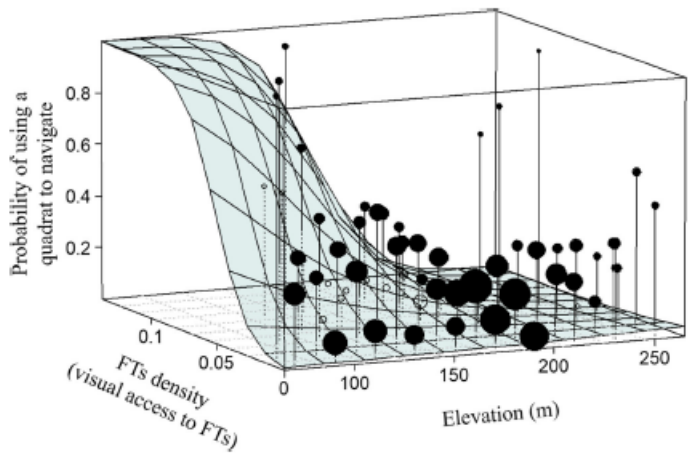

Fig. 3 Probability that black howler monkeys selected a quadrat to navigate at least in four different occasions in relation to the relative elevation within their home range and FTs density (proxy for visual access to FTs). The height of spheres represents the probability that a certain quadrat was chosen to navigate per combination of elevation and FTs density. Each surface (i.e., square) represents the expected probability of a quadrat to be chosen according to the model (conditional on all other predictors being set at their average value). Sphere size corresponds to the relative number of observations, with closed circles being above the model surface and open circles below

combined increasing accessibility and monitoring of FTs while travelling along route segments. By securing foraging success while reducing the number of locations that need to be memorised, the complexity of processing movement decisions decreases [65, 67]. In addition, a reduction in the number of operative elements to include in the cognitive processes enhances the planning abilities of animals and humans [39, 68]. Specifically, arboreal primates have been shown to plan future movements using information obtained from monitoring feeding trees while travelling [69] or to re-direct their trajectories towards specific tree species after inspecting other trees from the same species [69, 70]. By gathering ecological information on patterns of food availability, animals increase the predictability of a successful foraging event across heterogeneous landscapes [67].

Black howlers navigated through elevated areas only under decreasing FTs density on route segments used on four different occasions or more (see Additional file 4: Figure S3). Likely, elevated areas increased black howlers' visual access over the landscape enhancing the detectability of faraway food resources. Arboreal primates in rainforests need to find strategies to enhance their visual window typically obstructed by foliage, tree trunks or lianas [71]. Here, we provide evidence for the first time that supports the use of elevated areas as a strategy to enhance information acquisition via visual cues of food resources, which was suggested in previous studies on arboreal primate navigation [38, 45, 72]. Spiegel & Crofoot [1] asserted that not only the information state of an individual will determine its movement patterns but also the acquisition of information while "on the move". The attention black howlers allocated to search in their environment likely increased by following habitual routes and selecting suitable terrain to navigate increasing the acquisition of information and enhancing their movement decisions [73]. Subsequent research should address adjustment in the spatial performance of animals following enhanced visual or olfactory cues *en route*.

Even though we predicted that black howlers at PNP would avoid slopes to economise the expenditure of energy, we found a positive trend on the selection of routes associated with increased slope. The energetic cost of travelling along slopes for a large bodied animal represents a major challenge at ground level [74] but it may not be the case in the trees. Contrarily, travelling through sharp slopes may increase visual access over the landscape as discussed above [38]. Hence, patterns found in terrestrial animals cannot be assumed in arboreal animals since arboreality may impose other energetic challenges [74]. Howlers' main locomotor strategy is quadrupedalism [75], which means that moving vertically (descending to the ground and re-ascending to the canopy) rather than horizontally increases the number and complexity of movements in which they engage [41]. Thus, selecting areas with a continuous horizontal substrate (i.e., the canopy) might be more energetically advantageous than avoiding a terrain's ground slopes [76]. Indeed, our results show a tendency of selecting areas in which to navigate that avoid proximity to gaps in the canopy, similar to other arboreal animals [41, 45]. By avoiding canopy gaps, black howlers improve their overall energetic balance facilitating their locomotion but may also reduce their exposure to pathogens and terrestrial predators [76].

Overall, black howlers' navigation behaviour suggests that the current location of their habitual route network is the result of an optimization process to counteract the effect of different landscape attributes. Jang et al. [16] argued that the low visibility and widely distributed food sources of rainforests might have driven the development of extensive spatial knowledge and memory of food locations both in chimpanzees and human hunter-gatherers. Similarly, black howlers evolved strategies to enhance their visibility in rainforests and ease the acquisition of food resources. We argue that the accumulation of information through generations within social units could provide black howlers a strategy to progressively adjust the location of their routes to engage in efficient movement patterns [1]. Here, we provide evidence that efficient navigation can be achieved by travelling through habitual route networks but it is essential that future research addresses the optimisation process leading route's location to fully understand the role of information accumulation and sharing in movement ecology.

Conclusions

Route networks are advantageous mechanisms for arboreal animals to navigate and locate food resources in rainforests. Black howler's route network at our field site allowed them to visually intercept a high number of food resources while travelling, which potentially reduced their cognitive load and facilitated resource monitoring. Similarly, the importance of visual access to food resources was also shown by the tendency of black howler monkeys to travel through highly used route segments in elevated areas only under conditions of limited visual access to food resources. Arboreality imposed howlers to travel through areas void of canopy gaps, which potentially reduced the energetic costs of crossing gaps. The present study is the first fine-scale analyses addressing the influence of landscape features on arboreal animal movement patterns. Due to the dynamic nature of rainforests, future studies should consider the temporal component of route networks which may potentially mirror intra- and interannual fluctuations of rainforests.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s40462-019-0187-z.

Additional file 1: Table S1. Total feeding time and overall percentage of time spent by black howler monkeys on the top ten tree species at Palenque National Park. **Table S2.** Clustering analyses to determine the spatial patterns of black howler monkey's preferred tree species. **Table S3.** The comparison between the number of real FTs and simulated locations that fell within a series of buffers between 5 and 20 metres traced from the route networks of the study groups was always significant. **Table S4.** Results of the LMM testing differences among the number of locations computationally simulated and marked FT that fell within the visual detection distance of black howler monkeys. **Table S5.** Results of the LMM testing for differences in the number of FTs visually intercepted per meter travelled along route segments with different usage frequency (e.g., twice, 3 times, … until 9 times). **Table S6.** Results of the full GLMM testing the influence of different landscape attributes. **Table S7.** Random slopes and estimated variance components (standard deviations) for the random effects and residuals from the model testing the influence of landscape attributes on the occurrence of routes used at least twice within a quadrant. **Table S8.** Results of the full GLMM testing the influence of different landscape attributes (slope, presence of canopy gaps, elevation and visibility of feeding trees[1]) on the occurrence of a route segment used at least four times within a certain quadrat. **Table S9.** Random slopes and estimated variance components (standard deviations) for the random effects and residuals from the model testing the influence of landscape attributes on the occurrence of routes used at least four times within a quadrant.

Additional file 2: Figure S1. Graphic description of the method used to estimate black howler monkey's potential visibility of food resources throughout their home range.

Additional file 3: Figure S2. Three-dimensional representation of Palenque National Park and the study groups of black howler monkeys.

Additional file 4: Figure S3. Probability that black howler monkeys selected a quadrat to navigate in between three and height different occasions in relation to the relative elevation within their home range and the visibility of FT.

Abbreviations

d: Days; DEM: Digital Elevation Model; FTs: Feeding Trees; GLMM: Generalized Linear Mixed Model; h: Hours; ha: Hectares; KDE: Kernel Density Estimator; m: Metres; PNP: Palenque National Park; SD: Standard deviation; S.E. Standard error

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Authors' contributions

The overall research on the navigation of black howler monkeys was designed by SVB and AE. Data collection was performed by SVB, MdG and field assistants. Data analysis was performed by MdG. The manuscript was written by MdG and revised by SVB, AE and AN. All authors gave final approval for publication.

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Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

The present research does not include human participants, so this section is not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

[1]Department of Social Sciences, Oxford Brookes University, Gibbs Building, Gipsy Lane, Oxford OX3 0BP, UK. [2]Institute of Biology, National Autonomous University of Mexico, Mexico City, Mexico. [3]Department of Anthropology, University of Texas at Austin, Austin, TX, USA.

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References

1. Spiegel O, Crofoot MC. The feedback between where we go and what we know — information shapes movement, but movement also impacts information acquisition. Curr Opin Behav Sci. 2016;12:90–6.
2. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, et al. A movement ecology paradigm for unifying organismal movement research. Vol. 105, Proceedings of the National Academy of Sciences of the United States of America. 2008. p. 19052–19059.
3. Shepard ELC, Wilson RP, Gareth Rees W, Grundy E, Lambertucci SA, Vosper SB. Energy landscapes shape animal movement ecology. Am Nat. 2013; 182(3):298–312.
4. Gallistel CR. The organization of learning. Cambridge, MA: The MIT Press; 1990.
5. Hirtle SC, Heidorn PB. The structure of cognitive maps: representations and processes. In: Advances in Psychology. 1993. p. 170–192.
6. Bennett ATD. Do animals have cognitive maps? J Exp Biol. 1996;199:219–24.
7. McNaughton BL, Battaglia FP, Jensen O, Moser EI, Moser M-B. Path integration and the neural basis of the "cognitive map.". Nat Rev Neurosci. 2006;7(8):663–78.
8. Chrastil ER, Warren WH. From cognitive maps to cognitive graphs. Sutherland R, editor. PLoS One. 2014;9(11):e112544.
9. Normand E, Boesch C. Sophisticated Euclidean maps in forest chimpanzees. Anim Behav. 2009;77(5):1195–201.
10. Cheeseman JF, Millar CD, Greggers U, Lehmann K, Pawley MDM, Gallistel CR, et al. Way-finding in displaced clock-shifted bees proves bees use a cognitive map. Proc Natl Acad Sci U S A. 2014;111(24):8949–54.
11. Presotto A, Fayrer-Hosken R, Curry C, Madden M. Spatial mapping shows that some African elephants use cognitive maps to navigate the core but not the periphery of their home ranges. Anim Cogn. 2019;22(2):251–63.
12. Wehner R, Wehner S. Insect navigation: use of maps or Ariadne's thread? Ethol Ecol Evol. 1990;2(1):27–48.
13. Guilford T, Biro D. Route following and the pigeon's familiar area map. J Exp Biol. 2014;217(2):169–79.
14. Newmark WD, Rickart EA. High-use movement pathways and habitat selection by ungulates. Mamm Biol. 2012;77(4):293–8.
15. Trapanese C, Meunier H, Masi S. What, where and when: spatial foraging decisions in primates. Biol Rev. 2019;94(2):483–502.
16. Jang H, Boesch C, Mundry R, Ban SD, Janmaat KRL. Travel linearity and speed of human foragers and chimpanzees during their daily search for food in tropical rainforests. Sci Rep. 2019;9(11066).
17. Milton K. Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. Am Anthropol. 1981;83:534–48.
18. Di Fiore A, Suarez SA. Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. Anim Cogn. 2007;10(3):317–29.

19. Sasaki T, Biro D. Cumulative culture can emerge from collective intelligence in animal groups. Nat Commun. 2017;8:15049.
20. Jesmer BR, Merkle JA, Goheen JR, Aikens EO, Beck JL, Courtemanch AB, et al. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. Science (80-). 2018;361(6406):1023–5.
21. Couzin ID. Collective cognition in animal groups. Trends Cogn Sci. 2009; 13(1):36–43.
22. Vittori K, Talbot G, Gautrais J, Fourcassié V, Araújo AFR, Theraulaz G. Path efficiency of ant foraging trails in an artificial network. J Theor Biol. 2006; 239(4):507–15.
23. Denny CK, Stenhouse GB, Nielsen SE. Scales of selection and perception: landscape heterogeneity of an important food resource influences habitat use by a large omnivore. Wildl Biol. 2018;2018(1):1–10.
24. Howard AM, Nibbelink NP, Madden M, Young LA, Bernardes S, Fragaszy DM. Landscape influences on the natural and artificially manipulated movements of bearded capuchin monkeys. Anim Behav. 2015;106:59–70.
25. Avgar T, Baker JA, Brown GS, Hagens JS, Kittle AM, Mallon EE, et al. Space-use behaviour of woodland caribou based on a cognitive movement model. J Anim Ecol. 2015;84(4):1059–70.
26. Bertolani P. Ranging and travelling patterns of wild chimpanzees at Kibale, Uganda:a GIS approach: University of Cambridge (UK); 2013.
27. Janmaat KRL, Ban SD, Boesch C. Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. Anim Behav. 2013;86(6):1183–205.
28. Dollins FL, Mitchell RW. Spatial cognition, spatial perception: mapping the self and space. Cambridge: Cambridge University Press; 2010.
29. Killian NJ, Jutras MJ, Buffalo EA. A map of visual space in the primate entorhinal cortex. Nature. 2012;491 (7426):761–4.
30. Gallotti R, Porter MA, Barthelemy M. Lost in transportation: Information measures and cognitive limits in multilayer navigation. Sci Adv. 2016;2(2):e1500445.
31. Buzsáki G, Moser EI. Memory, navigation and theta rhythm in the hippocampal-entorhinal system. Nat Neurosci. 2013;16(2):130–8.
32. Dicke U, Roth G. Neuronal factors determining high intelligence. Philos Trans R Soc B. 2016;371(1685):20150180.
33. Isler K, van Schaik CP. Metabolic costs of brain size evolution. Biol Lett. 2006; 2(4):557–60.
34. Halsey LG. Terrestrial movement energetics: current knowledge and its application to the optimising animal. J Exp Biol. 2016;219(10):1424–31.
35. Wall J, Douglas-Hamilton I, Vollrath F. Elephants avoid costly mountaineering. Curr Biol. 2006;16(14):R528–9.
36. Thorpe SKS, Crompton RH, Alexander RM. Orangutans use compliant branches to lower the energetic cost of locomotion. Biol Lett. 2007;3(3): 253–6.
37. Reilly MC, Suarez SA. Patterns of habitat use and ranging behavior of squirrel monkeys (*Saimiri sciureus*) in the Yasuni National Park, Ecuador. Am J Phys Anthropol. 2010;50(Supplement):197.
38. Gregory T, Mullett A, Norconk MA. Strategies for navigating large areas: a GIS spatial ecology analysis of the bearded saki monkey, *Chiropotes sagulatus*, in Suriname. Am J Primatol. 2014;76(6):586–95.
39. Fagan WF, Lewis MA, Auger-M Eth M, Avgar T, Benhamou S, Breed G, et al. Spatial memory and animal movement. Ecol Lett. 2013;16:1316–29.
40. Crête M, Larivière S. Estimating the costs of locomotion in snow for coyotes. Can J Zool. 2003;81(11):1808–14.
41. McLean KA, Trainor AM, Asner GP, Crofoot MC, Hopkins ME, Campbell CJ, et al. Movement patterns of three arboreal primates in a Neotropical moist forest explained by LiDAR-estimated canopy structure. Landsc Ecol. 2016; 31(8):1849–62.
42. Halsey LG, Coward SRL, Crompton RH, Thorpe SKS. Practice makes perfect: performance optimisation in 'arboreal' parkour athletes illuminates the evolutionary ecology of great ape anatomy. J Hum Evol. 2017;103:45–52.
43. Dias PA, Rangel-Negrín A. Diets of howler monkeys. In: Kowalewski MM, Garber PA, Cortes-Ortiz L, Urbani B, Youlatos D, editors. Howler monkeys: adaptive radiation, systematics, and morphology. New York: Springer New York; 2015. p. 21–56.
44. Amato KR, Righini N. The howler monkey as a model for exploring host-gut microbiota interactions in primates. In: Kowalewski MM, Garber PA, Cortes-Ortiz L, Urbani B, Youlatos D, editors. Howler monkeys: adaptive radiation, systematics, and morphology. New York: Springer New York; 2015. p. 229–58.
45. Hopkins ME. Mantled howler (*Alouatta palliata*) arboreal pathway networks: relative impacts of resource availability and forest structure. Int J Primatol. 2011;32(1):238–58.
46. Barnhart EL. The Palenque mapping project: settlement and urbanism at an ancient Maya city: University of Texas at Austin (USA); 2001.
47. Estrada A, Mendoza A, Castellanos L, Pacheco R, Van Belle S, García Y, et al. Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, Mexico. Am J Primatol. 2002;58(2):45–55.
48. Van Belle S, Estrada A, Garber PA. Collective group movement and leadership in wild black howler monkeys (*Alouatta pigra*). Behav Ecol Sociobiol. 2013;67(1):31–41.
49. Calenge C. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model. 2006;197:516–9.
50. IUCN. The IUCN Red List of Threatened Species. Version 2019–2. 2019.
51. Presotto A, Izar P. Spatial reference of black capuchin monkeys in Brazilian Atlantic Forest: egocentric or allocentric? Anim Behav. 2010;80(1):125–32.
52. Garber PA, Porter LM. Navigating in small-scale space: the role of landmarks and resource monitoring in understanding saddleback tamarin travel. Am J Primatol. 2014;76(5):447–59.
53. Bebko AO. Ecological and cognitive influences on orangutan space use. York University (Canada); 2018.
54. Janmaat KRL, Boesch C, Byrne R, Chapman CA, Goné Bi ZB, Head JS, et al. Spatio-temporal complexity of chimpanzee food: how cognitive adaptations can counteract the ephemeral nature of ripe fruit. Am J Primatol. 2016;78(6): 626–45.
55. Suarez SA, Kairo J, Kiper J, Farfer D, McElroy B, Rogers, BC, Stockwell B, Young T. A comparison of computer-generated and naturally occurring foraging patterns in route-network-constrained spider monkeys. Am J Primatol. 2014;76(5):460–71.
56. Bivand R, Keitt T, Rowlingson B. rgdal: Bindings for the "Geospatial" Data Abstraction Library. 2018.
57. Clark PJ, Evans FC. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology. 1954;35(4):445–53.
58. Huisman O, De By RA. Principles of geographic information systems. In: Huisman O, De By RA, editors. Spatial data analysis. Enschede: ITC; 2009. p. 411–415.
59. Roy DP, Wulder MA, Loveland TR, C.E. W, Allen RG, Anderson MC, et al. Landsat-8: science and product vision for terrestrial global change research. Remote Sens Environ. 2014;145:154–72.
60. Bates D, Maechler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. J Stat Softw. 2014;67(1):1–48.
61. Van Belle S, Estrada A. The influence of loud calls on intergroup spacing mechanism in black howler monkeys (*Alouatta pigra*). Int J Primatol. 2019 (in press).
62. Fürtbauer I, Mundry R, Heistermann M, Schülke O, Ostner J. You mate, I mate: macaque females synchronize sex not cycles. Santos L, editor. PLoS One. 2011;6(10):e26144.
63. Fox J, Weisberg S. Multivariate linear models in R. In: Salmon H, O'Heffernan M, DeRosa K, Dickens G, editors. An R companion to applied regression. Los Angeles: SAGE Publications; 2018. p. 173–435.
64. Barr DJ, Levy R, Scheepers C, Tily HJ. Random effects structure for confirmatory hypothesis testing: Keep it maximal. J Mem Lang. 2013;68(3):255–78.
65. Poucet B. Spatial cognitive maps in animals: new hypotheses on their structure and neural mechanisms. Psychol Rev. 1993;100(2):163–82.
66. Berdahl AM, Kao AB, Biro D, Flack A, Westley PAH, Codling EA, et al. Collective animal navigation and migratory culture: from theoretical models to empirical evidence. Philos Trans R Soc B. 2018;373(1746):20170009.
67. Janson CH. Foraging benefits of ecological cognition in fruit-eating primates: results from field experiments and computer simulations. Front Ecol Evol. 2019;7:125.
68. Terrace HS. The comparative psychology of chunking. In: Fountain SB, Bunsey MD, Danks JH, McBeath MK, editors. Animal cognition and sequential behavior. Boston, MA: Springer USA; 2002. p. 23–55.
69. Janmaat KRL, Chapman CA, Meijer R, Zuberbühler K. The use of fruiting synchrony by foraging mangabey monkeys: a 'simple tool' to find fruit. Anim Cogn. 2012;15(1):83–96.
70. Ban SD, Boesch C, N'Guessan A, N'Goran EK, Tako A, Janmaat KRL. Tai chimpanzees change their travel direction for rare feeding trees providing fatty fruits. Anim Behav. 2016;118:135–47.
71. Janson CH, Bitetti MSD. Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. Behav Ecol Sociobiol. 1997;41(1):17–24.
72. Warren WH. Non-Euclidean navigation. J Exp Biol. 2019;222(Suppl 1): jeb187971.

73. Janson CH, Byrne R. What wild primates know about resources: Opening up the black box. Anim Cogn. 2007;10:357–67.
74. Halsey LG, White CR. A different angle: comparative analyses of whole-animal transport costs when running uphill. J Exp Biol. 2017;220(2):161–6.
75. Youlatos D, Couette S, Halenar LB, Youlatos D, Couette S, Halenar LB. Morphology of howler monkeys: a review and quantitative analyses. In: Kowalewski MM, Garber PA, Cortes-Ortiz L, Urbani B, Youlatos D, editors. Howler monkeys: adaptive radiation, systematics, and morphology. New York: Springer New York; 2015. p. 133–76.
76. Ancrenaz M, Sollmann R, Meijaard E, Hearn AJ, Ross J, Samejima H, et al. Coming down from the trees: is terrestrial activity in Bornean orangutans natural or disturbance driven? Sci Rep. 2015;21(5):487–99.

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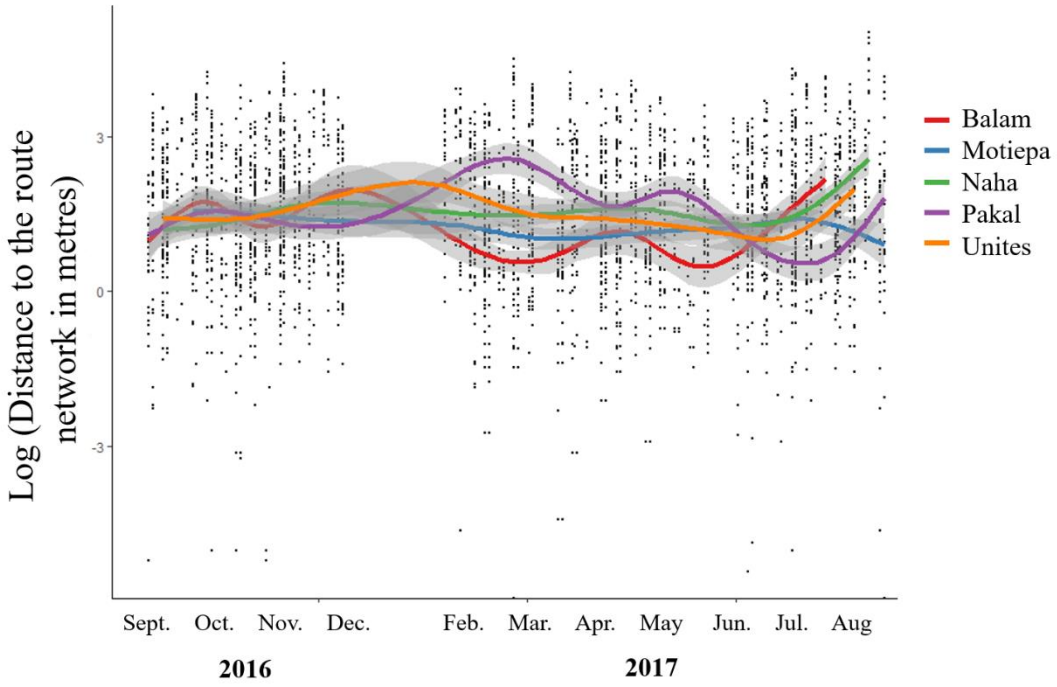
Appendix III



Appendix III. Figure 1. Mean (±SD) deviation from the route network throughout the study period per study group. I generated all route networks using just half of the data (i.e., two days a week) and calculated its deviation from the other half of the data (i.e., the other two days of that sane week) using the nearest neighbour analysis in QGIS 3.0. I aimed to use this measure as an estimation for route reliance throughout the study period.

Appendix IV

Appendix IV. Table 1. Probability of performing directional changes at loud calling locations.

Full null model comparison	$\chi^2 = 20.12$, d.f. = 7, *p*-value = 0.005				
Predictor variable	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	***p*-value**
(Intercept)	-4.09	0.743	-5.546	-2.634	
Context (spontaneous vs. IGE)	-0.722	0.689	-2.073	0.630	0.295
Altitude	0.476	0.313	-0.137	1.090	0.128
Overlapping area	0.120	0.692	-1.236	1.476	0.862
Times loud calling at that location before	0.779	0.288	0.215	1.343	0.007
Occurrence of IGE at that location before	1.886	0.655	0.603	3.169	0.004
Context * Altitude	-0.283	0.627	-1.511	0.946	0.652
Context * Overlapping area	-0.452	1.523	-3.437	2.534	0.767

Appendix IV. Table 2. Probability of performing directional changes before loud calling locations

Full null model comparison	$\chi^2 = 3.905$, d.f. = 7, *p*-value = 0.791				
Predictor variable	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	***p*-value**
(Intercept)	-3.308	0.780	-4..836	-1.780	
Context (spontaneous vs. IGE)	-0.159	0.588	-1.312	0.994	0.795
Altitude	0.051	0.317	-0.571	0.673	0.874
Overlapping area	-0.176	0.962	-2.061	1.709	0.851
Times loud calling at that location before	0.124	0.312	-0.488	0.736	0.693
Occurrence of IGE at that location before	0.416	0.568	-0.697	1.530	0.482
Context * Altitude	0.646	0.633	-0.595	1.886	0.308
Context * Overlapping area	-2.121	1.609	-5.273	1.033	0.187

Appendix IV. Table 3. Probability of performing directional changes at feeding locations.

Full null model comparison	$\chi^2 = 7.727$, d.f. = 2, *p*-value = 0.021				
Predictor variable	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	***p*-value**
(Intercept)	-2.684	0.276	-3.225	-2.144	
Item	-1.288	0.720	-2.700	0.054	0.021

Appendix IV. Table 4. Probability of performing directional changes before feeding locations.

Full null model comparison	$\chi^2 = 5.455$, d.f. = 2, *p*-value = 0.066				
Predictor variable	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	***p*-value**
(Intercept)	-2.028	0.201	-2.422	-1.634	
Item	-0.675	0.442	-1.541	-0.199	0.066

Appendix IV. Table 5. Probability of performing directional changes before feeding on young leaves related with the spatiotemporal characteristics of the area.

Response variable	**Probability of performing a directional change at young leaves feeding sites**				
Full null model comparison	$\chi^2 = 0.619$, d.f. = 3, *p*-value = 0.892				
Predictor variable	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	***p*-value**
(Intercept)	-8.908	2.751	-14.299	-3.516	[a]
Synchrony	-0.389	3.947	-8.125	7.348	0.922
Preferred tree	-1.720	7.646	-16.705	13.265	0.822
Synchrony * Preferred tree	-1.327	23.726	-47.829	45.176	0.706
Response variable	**Probability of performing a directional change before young leaves feeding sites**				
Full null model comparison	$\chi^2 = 12.781$, d.f. = 3, *p*-value = 0.005				
Predictor variable	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	***p*-value**
(Intercept)	-3.104	0.536	-4.155	-2.054	[a]
Synchrony	[b]	[b]	[b]	[b]	[b]
Preferred tree	[b]	[b]	[b]	[b]	[b]
Synchrony * Preferred tree	-0.534	1.132	-2.752	1.685	0.637

[a] Not shown because of having no meaningful or very limited interpretation.

[b] Not shown because the model due to converge as a consequence of the limited sample size in the response variable.

Appendix IV. Table 6. Probability of performing directional changes before feeding on fruits related with the spatiotemporal characteristics of the area.

Response variable	**Probability of performing a directional change at fruit feeding sites**				
Full null model comparison	$\chi^2 = 5.613$, d.f. = 3, *p*-value = 0.132				
Predictor variable	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	***p*-value**
(Intercept)	-3.908	0.816	-5.409	-2.210	[a]
Synchrony	-0.159	0.416	-0.975	0.657	0.698
Preferred tree	0.907	0.665	-0.396	2.209	0.116
Synchrony * Preferred tree	1.613	0.870	-0.091	3.317	0.088
Response variable	**Probability of performing a directional change before fruit feeding sites**				
Full null model comparison	$\chi^2 = 4.154$, d.f. = 3, *p*-value = 0.245				
Predictor variable	**Estimate**	**SE**	**CI_{lower}**	**CI_{upper}**	***p*-value**
(Intercept)	-6.808	1.789	-10.314	-3.301	[a]
Synchrony	-0.077	1.039	-2.113	1.958	0.941
Preferred tree	1.145	2.123	-3.016	5.307	0.590
Synchrony * Preferred tree	0.429	1.980	-3.452	4.309	0.829

[a] Not shown because of having no meaningful or very limited interpretation.